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Fishery Bulletin

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A retrospective (1979–1996) multispecies assessment of coral reef fish stocks in the Florida Keys

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Abstract.–A baseline assessment of 35 economically and ecologically important Florida Keys reef fish stocks is provided by using a systems approach that integrates sampling, statistics, and mathematical modeling. Quantitative fishery-independent data from reef fish visual surveys conducted by SCUBA divers from 1979 to 1996 were used to develop estimates of population abundance, assemblage composition, and stock structures in relation to key physical and habitat factors. Exploitation effects were assessed with a new length-based algorithm that calculates total mortality rates from estimates of "average length of fish in the exploitable phase of the stock." These estimates were highly correlated for two statistically independent data sources on reef fish: fishery-independent diver observations and fishery-dependent head boat catches. We developed a reef fish equilibrium exploitation fishery simulation (REEFS) model and used estimates of fishing mortality to assess yield-per-recruit in relation to fishing intensity and gear selectivity and to assess spawning potential ratio (SPR) in relation to U.S. federal "overfishing" standards. Our analyses show that 13 of 16 groupers (Epinephelinae), 7 of 13 snappers (Lutjanidae), one wrasse (Labridae), and 2 of 5 grunts (Haemulidae) are below the 30% SPR overfishing minimum. Some stocks appear to have been chronically overfished since the late 1970s. The Florida Keys reef fishery exhibits classic "serial overfishing" in which the largest, most desirable, and vulnerable species are depleted by fishing. Rapid growth of the barracuda population (Sphyraenidae) during the same period suggests that fishing has contributed to substantial changes in community structure and dynamics.

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The Florida Keys support a rich tropical marine ecosystem, a productive multispecies coral reef fishery, and a billion dollar tourist economy. The Florida Keys are also considered an "ecosystem-at-risk" as one of the nation's most significant yet most stressed marine resources under management of the National Oceanic and Atmospheric Administration (NMFS, 1996). Concern about habitat degradation and escalating resource uses from a rapidly growing human population in southern Florida resulted in the establishment of the Florida Keys National Marine Sanctuary (FKNMS) in 1990. Because they are one of the most complex ecosystems on earth, coral reefs are a particular concern. The diverse fish community of these coral reefs is influenced by complicated biological and physical interactions (Sale, 1991; Lee et al., 1992; Polunin and Roberts, 1996). Reef fisheries can target a number of economically and ecologically important species (e.g. groupers, snappers, lobsters, conch, sponges, and corals). Over the past several decades, public use of and conflicts over fishery resources have increased sharply, while some fishery catches from historically productive snapper and grouper stocks have declined (Bohnsack et al., 1994). Concomitantly, the status and biological dynamics of these reef fishery resources are not well understood, and important stock assessment data are not available.

Another concern regarding reef fishery resources is the restoration of the Everglades north of the Florida Keys. Hydrological projects of historic proportions are expected to make a substantial change in the timing, volume, and location of freshwater outflows into the coastal marine environment (Harwell et al., 1996). These changes could affect the survivorship of juvenile reef fishes in critical shallow nursery areas of Florida Bay and Biscayne Bay and ultimately affect the productivity of the entire coral reef ecosystem.

The condition of most reef fish stocks is unknown because of the large number of species in the fishery, a lack of fishery-effort and landings data, and the quantity of population dynamics data needed to do traditional stock assessments. The goal of this paper is to develop a technically sound quantitative method for multispecies management assessments. For this purpose, we present an integrated baseline assessment to reference the status of the multispecies fishery so that the effects of management changes in the FKNMS may be accurately evaluated in the future (U.S. Dep. Commerce, 1996). Using fishery-independent data, we conducted an 18-year retrospective, analytical yield assessment of economically important Florida Keys reef fish stocks to elucidate the effects of fishing and to help define an effective fishery management strategy.

Hypothesis

A key to our ability to assess reef fish stocks was the use of "average size" (in length) of fish in the exploitable phase of the population ($\bar{L}$) as an indicator of stock status. Average size of fish was derived from visual survey data or headboat landings data. Headboats are party boats that carry more than 15 anglers per fishing trip (Dixon and Huntsman[1]). The use of $\bar{L}$ in stock assessment has deep roots in traditional fisheries management (Beverton and Holt, 1956, 1957; Ricker, 1975). The statistic provides a population level metric that integrates individual metabolic variables such as interdependent growth, mortality, and reproductive processes. The $\bar{L}$ statistic also is an important index of fishing effects because persistent heavy fishing reduces the average size of the population over time, making the stock younger through a process known as "juvenescence" which successively eliminates older, more fecund size classes (Ricker, 1963). This is extremely important in the context of stock and recruitment because the fecundity potential of individuals increases exponentially with size. In general, the average length of fish in the exploitable phase (i.e. between the size at first capture, L', and the maximum size, L_λ) is highly correlated with average population size and thus reflects the rate of fishing mortality operating in the fishery.

Theoretically, the average size of fish landed for any given species should be equal to the average size in the exploited phase of the remaining population just after fishing. In other words, we hypothesize that fishery-independent survey estimates of average length derived from visual data reported by divers should equal fishery-dependent estimates derived from catch data reported by headboat anglers. The greater the correlation between the two independent estimates of $\bar{L}$, the more robust "average length" should be as an indicator of stock status subject to exploitation.

[1] Dixon, R. L., and G. R. Huntsman. 1992. Estimating catches and fishing effort of the southeast United States headboat fleet, 1972–1982. Beaufort Laboratory, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Beaufort, NC 28516. Draft report.

Methods and materials

Study area

The Florida Keys coral reef ecosystem is a unique tropical coastal marine environment stretching about 370 km from Key Biscayne southwest to the Dry Tortugas (Fig. 1). Situated parallel to the Florida current and Florida Bay, the coastal ecosystem encompasses many varied habitats comprising fresh- to saltwater marshes, estuaries, lagoons, mangrove stands, coral islands, sea grass beds, and coral reefs. Florida Bay and adjacent coastal estuaries serve as nursery areas for spiny lobster and many juvenile fishes that occupy reefs as adults. The clear water and high diversity of reef fish in the Florida Keys coral reef tract provide a unique environment to assess multispecies fisheries. Here we use a "systems approach" to facilitate effective decision making and to improve fishery management performance (Ault and Fox, 1989; Rothschild et al., 1996).

Reef fish surveys

Fishery-independent visual estimates of the abundance and size distributions of multispecies reef fish populations were taken along the Florida Keys reef track continuously from 1979 to 1996 (Table 1) by 12 highly trained and experienced divers using the stationary visual survey method of Bohnsack and Bannerot (1986). This nondestructive method provides reliable quantitative estimates of species abundance, frequency-of-occurrence, and size structure for the reef fish community. Divers recorded the abundance as well as the minimum, mean, and maximum lengths of each species seen during 5 minutes within randomly selected 7.5-m radius circular quadrats. Underwater visual estimates of reef fish size and abundance have frequently been made (Bellwood and Alcala, 1988; Harvey and Shortis, 1996); however, accurate and precise visual estimates of fish length require well-trained and experienced observers because objects in water appear magnified and closer than their actual range (Bell et al., 1985; Harvey and

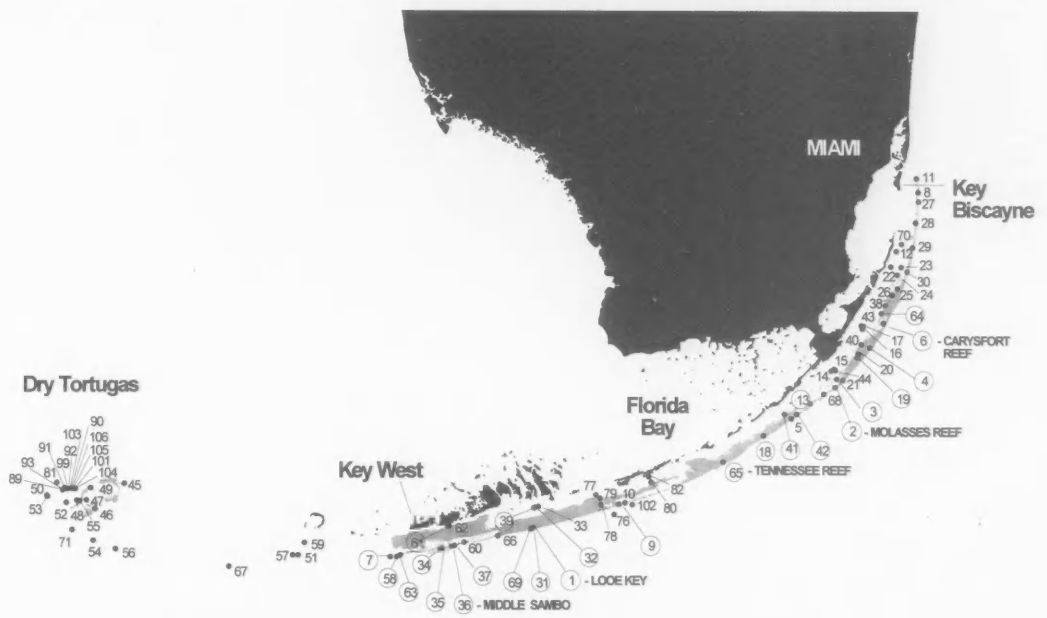

Figure 1

Map of the Florida Keys coastal marine ecosystem showing the coral reef tract (light gray) running offshore from Key Biscayne southwest to the Dry Tortugas, and the spatial relationships of Florida Bay, Key West, and the Miami urban center. Numbered darkened circles show the 89 reefs where 4,571 visual survey samples of the reef fish community were taken from 1979 to 1996. Open circles around numbers indicate sanctuary preservation areas (SPAs).

Table 1

Visual survey sampling effort (number of point samples) by habitat areas and depth intervals conducted from 1979 to 1996 in the Florida Keys reef tract. The offshore zone is exposed to the Florida Current.

Depth		Reef zone habitat type							
		Artificial reef	Coral reef		Hard bottom		Sand bottom	Totals	
Feet	Meters	Inshore	Inshore	Offshore	Inshore	Offshore	Inshore	Total	Percent
0–10	0–3.05	0	848	171	26	8	13	1,066	23.32
10–20	3.05–6.10	5	726	816	14	207	38	1,806	39.51
20–30	6.10–9.14	85	403	561	4	146	0	1,199	26.23
30–40	9.14–12.19	28	31	92	0	40	0	191	4.18
40–50	12.19–15.24	9	9	81	0	48	0	147	3.22
50–60	15.24–18.29	0	15	65	0	47	0	127	2.78
60–70	18.29–21.34	0	1	34	0	0	0	35	0.77
Total		127	2,033	1,820	44	496	51	4,571	
Percent		2.78	44.48	39.82	0.96	10.85	1.12		100.00

Shortis, 1996). To improve accuracy, divers continuously calibrated their length estimates with a 30-cm ruler attached perpendicular to the far end of a meterstick. Divers without calibration sticks have been shown to obtain a mean accuracy of 86% for length estimates (St. John et al., 1990).

Maximum use of the visual survey data required statistical intercalibration of the sampling efficiency of each diver. We used multiple regression analysis (Neter et al., 1996) to estimate relative sampling efficiency by adapting the "fishing power" model of Robson (1966)

$$C(d,t) = F(d,t)N(t)\xi(d,t) = q(d)f(d,t)N(t)\xi(d,t)$$
$$\rightarrow \frac{C(d,t)}{f(d,t)} = q(d)\overline{N}(d,t), \quad (1)$$

where $C(d,t)$ = the fish count of diver d at reef date t;
$N(t)$ = the average population size at reef date t;
$q(d)$ = the coefficient of sampling efficiency for diver d;
$f(d,t)$ = the nominal survey effort of diver d at reef date t, and
$\xi(d,t)$ = a log normally distributed error variable.

To account for any sampling bias that may have been introduced by differences among divers, a simple log-linear transformation of Equation 1 makes it possible to obtain minimum variance estimates of relative sampling efficiency, given fish counts by species, by diver, and by reef date. Data used for model development were derived from a series of controlled experiments conducted during a 9-day sampling expedition to the Dry Tortugas during June 1994. A matrix of estimated efficiency coefficients for divers by species was used to adjust an individual diver's results in relation to a standard-normal diver, here the most experienced diver in the group. After standardization, all the individual visual "catch-per-unit-of-effort" measurements were comparable over time and space (Ault et al.[2]). Spatial and temporal patterns in abundance and correlative linkages to habitat types were qualitatively analyzed with 3-D visualization software (IDL, 1995) by reef site throughout the Florida Keys for various survey years. Multivariate statistical analysis (Johnson and Wichern, 1992; Venables and Ripley, 1994) was used to assess variance-covariance and correlation structures between reef fish density and selected environmental and fish community auxiliary covariates.

We also used the 1981–95 NMFS headboat catch-and-effort data (Bohnsack et al., 1994; Dixon and Huntsman, 1992) to provide fishery-dependent population estimates comparable to those from the visual survey. Headboat data provide total numbers of individuals in the catch as well as total weight in the catch by species by year.

[2] Ault, J. S., J. A. Bohnsack, and G. Meester. 1998. The relative fishing power of divers in tropical reef fish visual surveys. Unpubl. manuscript.

Stock assessment indicator variable

A stock assessment indicator variable is a quantitative measure that reflects the status of a population subjected to fishing or other environmental changes. Because reef fishes integrate aspects of the coastal ocean environment over their lifetime, a robust measure of population "health" or status can provide a sensitive indicator of direct and indirect stress on the stock, and perhaps on the regional marine ecosystem (Fausch et al., 1990). Population health for reef fish communities can best be described with the metabolic-based pool variable "average length in the exploitable phase of the stock." Therefore, to assess the health of each of the s stocks in the reef fish community over the past two decades, the statistic "average length in the exploitable phase of the stock," $\overline{L}(t)$, was found for each stock by integrating between the population age limits from t' (minimum age at first capture) to t_λ (oldest age in the stock), written as

$$\overline{L}(t) = \frac{F(t)\int_{t'}^{t_\lambda} N(a,t)L(a,t)da}{F(t)\int_{t'}^{t_\lambda} N(a,t)da}, \quad (2)$$

where $N(a,t)$ = abundance for age class a at time t;
$L(a,t)$ = length for class a at time t; and
$F(t)$ = the instantaneous fishing mortality rate at time t.

Estimates of the mean, variance, and 95% confidence interval of the mean were computed by the methods of Sokal and Rohlf (1969).

To estimate the annual total instantaneous mortality rate $Z(t)$ for each fish stock in each year t from population size structure and abundance statistics, we used a length-based method (Ault and Ehrhardt, 1991; Ehrhardt and Ault, 1992) particularly applicable to reef fish population dynamics

$$\left[\frac{L_\infty - L_\lambda}{L_\infty - L'}\right]^{\frac{Z(t)}{K}} = \frac{Z(t)\left(L' - \overline{L}(t)\right) + K\left(L_\infty - \overline{L}(t)\right)}{Z(t)\left(L_\lambda - \overline{L}(t)\right) + K\left(L_\infty - \overline{L}(t)\right)}, \quad (3)$$

where, L_λ = maximum size;
L' = the length at first capture;
$\overline{L}(t)$ = the average size in the exploitable phase in year t; and

K and L_∞ = parameters of the von Bertalanffy equation.

Thus, the only unknown variable in Equation 3 is the total mortality rate in year t, $Z(t)$, which can be estimated fairly easily with an iterative algorithm called LBAR (Ault et al., 1996). Finally, by assuming that M, the annual instantaneous rate of natural mortality, is known and constant for the interval Δt, we can estimate the fishing mortality rate as $\hat{F}(t) = \hat{Z}(t) - M$.

Reef fish exploited-population simulation model

To achieve a better understanding of the dynamics of multispecies tropical coral reef fish stocks, their response to exploitation, and the accuracy and precision of statistical estimates from the sampling surveys, we developed an object-oriented computer simulation model for exploited reef fish populations in the Florida Keys fishery (REEFS [reef fish equilibrium exploitation fishery simulator (Ault[3])]). The fundamental population-dynamic processes of growth, mortality, and recruitment are relatively similar for fishes of the temperate, boreal, and tropical seas; however, some distinct differences in rates exist for tropical marine fishes as reflected by quasicontinuous growth, protracted spawning and recruitment, and competition-based population dynamics (Ault and Fox, 1990; Sparre and Venema, 1992; DeMartini, 1993). To represent the continuous time dynamics of a tropical coral-reef fish population in the numerical model, following Ault and Olson (1996), we formalized the conservation law for population abundance as

$$dN(a,t) = \frac{\partial N(a,t)}{\partial a}da + \frac{\partial N(a,t)}{\partial t}dt = -Z(a,t)N(a,t)dt. \quad (4)$$

This partial differential equation expresses population age structure in terms of the average number of fish by age over time. The term $\partial N/\partial a$ is the contribution to the change in $N(a,t)$ resulting from individuals getting older. Because the variable a is tied stepwise to chronological age, for each time step t, a gets one unit older, so that $da/dt = 1$. This condition holds for $t > 0$ and $a > 0$. Equation 4 requires two conditions on $N(a,t)$: one initial condition for $N(0,t)$; and a boundary condition in age 0 tied to reproduction for $N(0,t)$. Integration of Equation 4 with a growth function allows efficient estimation of population biomass and average size in the stock over time. In the numerical model REEFS, we modified Equation 4 to a stochastic age-independent length-based population dynamics model to simulate efficiently the average or ensemble number at a given length for the entire population age structure as

$$\overline{N}(L) = \int_{t_r}^{t_\lambda} R(\tau - a)S(a)\Theta(a)P(L|a)da, \quad (5)$$

where $R(\tau-a)$ = recruitment lagged back to cohort birth date;
$S(a)$ = survivorship to age a;
$\Theta(a)$ = sex ratio at age a; and
$P(L|a)$ = the conditional probability of a fish being length L given that it is age a.

The ensemble average length L at age a is represented by the von Bertalanffy growth function. The conditional probability distribution for length and age was assumed to be bivariate normal.

The reported maximum age of fish in the stock t_λ (equal to a generation), usually obtained from age and growth studies by using either scales or otoliths, allows application of a convenient and consistent method to normalize the annual instantaneous natural mortality rate M to life span. First, we assume that $S(t_\lambda)$, the fraction of the initial cohort numbers surviving from recruitment t_r to the maximum age, can be expressed as

$$\frac{N(t_\lambda)}{N(t_r)} = S(t_\lambda) = e^{-M(t_\lambda - t_r)}. \quad (6)$$

Then, assuming an unexploited equilibrium, by setting the probability of survivorship of recruits to the maximum age to be 5% (i.e. $S(t_\lambda)=0.05$), and letting t_r be equal to 0, we rearranged Equation 6 in order to provide an estimate of the natural mortality rate

$$\hat{M} = \frac{-\ln[S(t_\lambda)]}{t_\lambda}. \quad (7)$$

Mortality and growth estimation in tropical fishery populations are normally approached from a size-based perspective because of difficulties in ageing fish. Average size can be converted to mean age by making two assumptions: 1) that age a maps directly into, or is a function of, size $L(a)$; and 2) that mean length-at-age from the von Bertalanffy equation can be inverted as

$$a = \frac{-\ln\left[\frac{L_\infty - L(a)}{L_\infty}\right]}{K} + t_0. \quad (8)$$

[3] Ault, J. S. 1998. Tropical coral reef fishery resource decision dynamics. Unpubl. manuscript.

Numbers-at-length were converted to numbers-at-weight for each species by means of simple allometric relationships.

Assessment of exploitation effects

The REEFS model was configured to assess two fishery management decision-making endpoints, yield-per-recruit (YPR) and spawning potential ratio (SPR). Fishery management endpoints are relatively robust measures of potential yields and recruitment. As such, they help to focus on biological (size) and fishing (intensity) controls for managing current and future fishery production. Because biomass $B(a,t)$ is the product of numbers-at-age multiplied by weight-at-age, yield in weight Y_w from a given species s was calculated as

$$Y_w(F,L',t) = F(t)\int_{L'}^{L_\lambda} B(L|a,t)\,dL = F(t)\int_{L'}^{L_\lambda} N(L|a,t)W(L|a,t)\,dL\,. \quad (9)$$

Yield-per-recruit (YPR) is then calculated by scaling yield to average recruitment from the right-hand side of the above equation. Spawning stock biomass (SSB, in metric tons [t]) is a measure of the stock's reproductive potential or capacity to produce newborn, ultimately realized at the population level as successful cohorts or year classes. Spawning stock biomass is obtained by integrating over individuals between the minimum size of first maturity, L_m, and maximum reproductive size (here assumed to be the maximum size L_λ) in the stock

$$SSB(t) = \int_{L_m}^{L_\lambda} B(L|a,t)\,dL. \quad (10)$$

The size of first capture, L', is that regulated by regional fishery management. The modeled fishing mortality rate of headboats (and "viewing power" of divers) was assumed to remove (and sight) fish with a "knife-edged selectivity pattern" (see Gulland, 1983) over the range of exploitable sizes

$$F(t) = \begin{cases} 0 & \text{if } L|a < L' \\ \hat{F}(t) & \text{if } L|a \geq L' \end{cases}. \quad (11)$$

Spawning potential ratio (SPR) is a contemporaneous management endpoint that measures the stock's potential capacity to produce optimum yields on a sustainable basis. SPR is a fraction expressed as the ratio of exploited spawning stock biomass in relation to the equilibrium unexploited SSB

$$SPR = \frac{SSB_{exploited}}{SSB_{unexploited}}. \quad (12)$$

Resultant estimated SPRs are then compared to the U.S. Federal standards which define 30% SPR as the "overfishing" threshold (Rosenberg et al., 1996). Linear regressions of estimated SPRs for snapper and grouper were made on 1996 average exvessel prices obtained from voluntary Monroe County dealer reports (NMFS[4]). Because sale of jewfish was prohibited, a theoretical 1996 jewfish price was estimated as 0.438 of the price of gag grouper on the basis of historical average annual price ratios (1987–90).

Management analyses

This assessment focuses on 35 reef fish species in 5 families: groupers, Epinephelinae; snappers, Lutjanidae; grunts, Haemulidae; the hogfish, *Lachnolaimus maximus*, Labridae; and the great barracuda, *Sphyraena barracuda*, Sphyraenidae. These are the primary targets of the recreational, commercial, and headboat fleets. Population dynamics parameters for each of these fish used in the analyses were gleaned from summaries in Claro (1994) and taxa-specific literature (Tables 2 and 3). The hogfish was grouped with snappers for analytical purposes.

The assessment used the following 7 steps (Fig. 2):

Step 1: Conduct visual survey for the reef fish community in year t and intercalibrate diver sampling efficiency by species, site, and year.

Step 2: Begin management analysis for species s using intercalibrated visual survey data to compute within-year estimates of $\bar{L}$ and associated 95% confidence intervals from the size and abundance data, by species, integrated over the range of exploitable sizes.

Step 3: Compute a statistically independent set of annual mean estimates of $\bar{L}$ using fishery-dependent headboat data and compare these with visual survey estimates.

[4] NMFS. 1996. Fishery Statistics Div., Southeast Fisheries Sci. Center, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami FL 33149-1003.

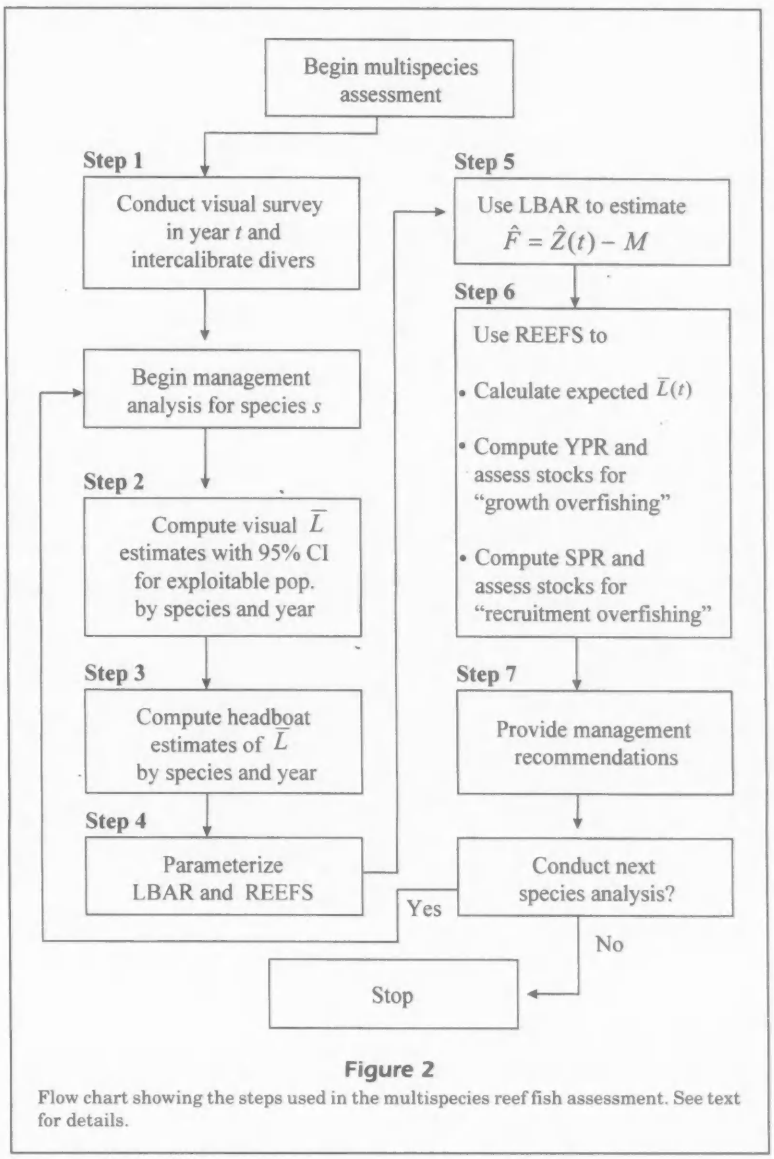
Begin multispecies assessment
Step 1
Conduct visual survey in year t and intercalibrate divers
Begin management analysis for species s
Step 2
Compute visual $\bar{L}$ estimates with 95% CI for exploitable pop. by species and year
Step 3
Compute headboat estimates of $\bar{L}$ by species and year
Step 4
Parameterize LBAR and REEFS
Step 5
Use LBAR to estimate $\hat{F} = \hat{Z}(t) - M$
Step 6
Use REEFS to
• Calculate expected $\bar{L}(t)$
• Compute YPR and assess stocks for "growth overfishing"
• Compute SPR and assess stocks for "recruitment overfishing"
Step 7
Provide management recommendations
Conduct next species analysis?
Yes
No
Stop

Figure 2

Flow chart showing the steps used in the multispecies reef fish assessment. See text for details.

Step 4: Use the population dynamics parameters of Table 3 to determine parameters of the LBAR (Ault et al., 1996) and the REEFS computer algorithms.

Step 5: Use $\bar{L}(t)$ estimate in LBAR to estimate by year fishing mortality rates for the two data sources; i.e. time series of visual and headboat data.

Step 6: Use the REEFS model to estimate: 1) expected $\bar{L}(t)$ given the reported population dynamics and $\hat{F}$ parameter values; 2) YPR and assess growth overfishing; and 3) spawning stock biomass (SSB) for the fishery in both exploited and unexploited states (i.e. $F = \hat{F}$, and $F=0$, respectively) and evaluate SPR to assess for recruitment overfishing.

Step 7: From these results, make specific fishery management recommendations on control strategies of F and L^c consistent with eumetric fishing principles that minimize the potential for overfishing.

Results

Fishing effort and sampling intensity

Trends in nominal fishing effort, measured as the numbers of licensed recreational, commercial, and headboats vessels in Monroe County, show that recreational fishing effort has increased sharply since 1965 (Fig. 3). Since 1981, the largest increase has clearly come from the recreational sector and continues to increase whereas commercial and headboat sectors have been relatively stable.

In the 18-year (1979–96) visual survey, 4,571 point samples were collected over a variety of bottom types from 72 reefs located throughout the Florida Keys at depths to 21 m (Table 1; Fig. 1). The complete database contains information on 226 reef fish species in 55 families with 42 biological, habitat, and physical covariates.

Table 2

Parameters, definitions, and units for population dynamics variables common to the LBAR and REEFS numerical models used in simulation analysis of Florida Keys reef fish population dynamics. See Table 3 for parameter values.

Parameter	Definition	Units
s	Reef fish species (s=1, . . . ,n)	
a	Cohort age class (a=1, . . . , t_λ)	
t_r	Age of recruitment	months
L_r	Size at recruitment	mm
t_m	Minimum age of maturity	months
L_m	Minimum size of maturity	mm
t'	Minimum age of first capture	months
L'	Minimum size of first capture	mm
t_λ	Oldest (largest) age	years
L_λ	Largest (oldest) size	mm
W_∞	Ultimate weight	kg
L_∞	Ultimate length	mm
K	Brody growth coefficient	per year
t_0	Age at which size equals 0	years
α_{WL}	Scalar coefficient of weight-length function	dimensionless
β_{WL}	Power coefficient of weight-length function	dimensionless
$W(a,t)$	Weight at age a at time t	g
$L(a,t)$	Length at age a at time t	mm
$N(a,t)$	Numbers at age a at time t	number of fish
$M(a,t)$	Natural mortality rate at age a at time t	per year
$F(a,t)$	Fishing mortality rate at age a at time t	per year
$S(a)$	Survivorship to age a	dimensionless
$Z(t)$	Total mortality rate in year t	dimensionless
$\Theta(a)$	Sex ratio at age a	dimensionless
$B(a,t)$	Biomass at age a in year t	kg
$Y_w(t)$	Yield in weight in year t	metric tons
$SSB(t)$	Spawning stock biomass in year t	metric tons
$SPR(t)$	Spawning potential ratio in year t	percent

Average size and mortality

Average annual length was estimated for headboat catch statistics (1981–95) and for visual survey data (1979–96). Headboat data were used in the comparative analysis with the visual survey data because they provide consistent catch statistics and effort data. Typical comparisons of average length in the exploitable phase of the stock for the two data sets are shown for eight representative, economically important reef fishes: black grouper, red grouper, gray snapper, yellowtail snapper, white grunt, bluestriped grunt, hogfish, and great barracuda (Fig. 4). The 95% confidence intervals were computed for the visual estimates but could not be determined for the headboat data at this time owing to the survey estimation procedures used to calculate total numbers and total weight for the entire Florida Keys. In a few instances (e.g. 1985 and 1986), the computed confidence bounds were large owing to low sample sizes, but these mean estimates still correlated well with the rest of the data.

The estimated average lengths in the exploitable phase from the two independent data sources were highly correlated for groupers, snappers, and grunts (Fig. 4). The trend in average size also was relatively flat over the last 18 years and close to L' (Fig. 4).

Although the relation between $\bar{L}$ for visual and headboat data was similar for all groupers, snappers, and grunts, it differed somewhat for hogfish and barracuda (Fig. 4, G and H). Average length ($\bar{L}$) for hogfish was consistently smaller in visual samples than in headboat landings. In both data sets, however, $\bar{L}$ declined in the early 1980s but has steadily increased since the late-1980s (F=3.96, df=9, P<0.0001) (Fig. 4G). Average length for barracuda increased significantly (F=2.2, df=10, P<0.018) in visual surveys but declined in headboat landings beginning in the early 1980s (Fig. 4H). Increased mean barracuda size in visual samples indicates that there has been a corresponding increase in abundance because larger $\bar{L}$ requires increased survival. In visual samples, barracuda are now the top ranked species in biomass among all Florida Keys reef fishes.

Table 3

Florida Keys reef fish population dynamics parameters for 46 species used in mortality estimations and fishery simulations. Population dynamics parameter definitions and units are given in Table 2. The symbol * indicates that the species is present in recreational catch but not headboat catches or the visual survey. The dash (—) indicates that insufficient population dynamic data were available to conduct a management analysis. Complete parameter sets were available for 35 species.

	Population parameters											
Species groups	M	t_λ	L_∞	W_∞	K	t_0	t_m	L'	t'	α_{wl}	β_{wl}	L_λ
Groupers (n=18)												
Black Grouper *Mycteroperca bonaci*	0.150	20	1200.0	31.6	0.160	–0.300	48	508.0	39	4.27E-06	3.2051	1153.1
Coney *Epinephelus fulvus*	0.180	17	698.9	1.5	0.145	–1.080	13	203.2	19	7.29E-05	2.5700	332.5
Gag Grouper *Mycteroperca microlepis*	0.200	13	1187.2	25.1	0.149	–0.802	60	508.0	36	1.21E-05	3.0305	1034.4
Graysby *Epinephelus cruentatus*	0.200	15	415.0	1.1	0.130	–0.940	36	203.2	52	1.22E-05	3.0439	362.5
Jewfish *Epinephelus itajara*	0.081	37	2394.0	244.9	0.054	–3.616	72	508.0	68	2.09E-05	2.9797	2328.0
Marbled Grouper * *Epinephelus inermis*	—	—	—	—	—	—	—	—	—	—	—	—
Misty Grouper * *Epinephelus mystacinus*	—	—	—	—	—	—	—	—	—	—	—	—
Nassau *Epinephelus striatus*	0.180	17	698.9	5.9	0.145	–1.080	83	508.0	95	3.83E-06	3.2292	648.2
Red Grouper *Epinephelus morio*	0.180	17	938.0	11.9	0.153	–0.099	48	508.0	61	1.13E-05	3.0350	869.0
Red Hind *Epinephelus guttatus*	0.180	17	392.7	1.1	0.207	–0.831	49	203.2	33	1.80E-04	2.6140	382.9
Rock Hind *Epinephelus adscensionis*	0.250	12	486.1	2.3	0.191	–2.160	48	203.2	9	6.00E-06	3.1930	453.3
Scamp *Mycteroperca phenax*	0.143	21	999.7	19.3	0.126	–1.357	48	508.0	52	2.02E-05	2.9932	932.2
Snowy Grouper *Epinephelus niveatus*	0.130	15	1091.3	19.5	0.113	–0.915	48	508.0	57	2.45E-05	2.9300	909.0
Speckled Hind *Epinephelus drummondhayi*	0.200	15	967.0	16.6	0.130	–1.010	48	508.0	58	1.11E-05	3.0730	861.0
Warsaw Grouper *Epinephelus nigritus*	0.080	41	2394.0	244.9	0.054	–3.616	48	508.0	68	2.09E-05	2.9797	2328.0
Yellowedge Grouper *Epinephelus flavolimbatus*	0.180	15	860.0	15.7	0.170	0.000	67	508.0	64	2.82E-05	2.9800	960.0
Yellowfin Grouper *Mycteroperca venenosa*	0.180	15	860.0	15.7	0.170	0.000	67	508.0	64	2.82E-05	2.9800	960.0
Yellowmouth Grouper *Mycteroperca interstitialis*	0.180	17	881.8	8.6	0.063	–9.030	36	508.0	56	2.58E-05	2.8937	710.7
Snappers (n=13) and hogfish (n=1)												
Black Snapper *Apsilus dentatus*	0.300	10	618.3	3.2	0.097	–1.728	29	203.2	30	4.52E-05	2.8146	418.4
Blackfin Snapper *Lutjanus buccanella*	0.230	9	729.7	2.4	0.084	–2.896	20	304.8	43	7.40E-06	2.9735	458.8
Cubera Snapper *Lutjanus cyanopterus*	0.150	20	1200.0	34.9	0.160	–0.300	28	304.8	19	1.32E-05	3.0601	910.0
Dog Snapper *Lutjanus jocu*	0.333	9	854.0	10.2	0.100	–2.000	28	304.8	30	4.28E-05	2.8574	790.0
Gray Snapper *Lutjanus griseus*	0.300	10	722.3	5.2	0.136	–0.863	24	254.0	29	3.05E-05	2.8809	556.2
Lane Snapper *Lutjanis synagris*	0.300	10	618.3	3.2	0.097	–1.728	29	203.2	30	4.52E-05	2.8146	418.4

continued

Table 3 (continued)

Species groups	Population parameters											
	M	t_λ	L_∞	W_∞	K	t_0	t_m	L'	t'	α_{wl}	β_{wl}	L_λ
Mahogony Snapper *Lutjanus mahogoni*	0.300	10	618.3	3.2	0.097	–1.728	29	304.8	64	8.18E-05	2.7190	418.4
Mutton Snapper *Lutjanus analis*	0.214	14	938.7	14.1	0.129	–0.738	24	304.8	29	1.57E-05	3.0112	797.8
Red Snapper *Lutjanus campechanus*	0.190	16	975.0	13.7	0.162	–0.010	28	508.0	55	2.04E-05	2.953	955.0
Schoolmaster *Lutjanus apodus*	0.250	12	570.0	3.3	0.180	0.000	20	254.0	40	2.04E-05	2.9779	503.8
Silk Snapper *Lutjanus vivanus*	0.230	9	781.1	9.3	0.092	–2.309	37	304.8	38	1.00E-05	3.1000	512.0
Vermillion Snapper *Rhomboplites aurorubens*	0.230	10	613.6	2.8	0.206	0.111	43	254.0	33	1.72E-05	2.9456	541.6
Yellowtail Snapper *Lutjanus chrysurus*	0.214	14	454.7	1.3	0.209	–0.712	24	304.8	56	7.75E-05	2.7180	433.4
Hogfish *Lachnolaimus maximus*	0.250	12	566.0	3.8	0.190	–0.776	18	203.2	20	2.55E-05	2.9700	439.0
Grunts (n=13) and barracuda (n=1)												
Black Margate *Anisotremus surinamensis*	—	—	—	—	—	—	33	203.2	—	2.39E-06	3.3916	—
Bluestriped Grunt *Haemulon sciurus*	0.500	6	289.6	0.47	0.484	–0.011	12	203.2	31	1.94E-05	2.9996	273.5
Caesar Grunt *Haemulon carbonarium*	—	—	—	—	—	—	27	203.2	—	1.29E-05	3.0559	—
Cottonwick *Haemulon melanurum*	—	—	—	—	—	—	27	203.2	—	2.52E-05	2.9527	—
French Grunt *Haemulon flavolineatum*	—	—	—	—	—	—	18	203.2	—	9.06E-06	3.1581	—
Margate *Haemulon album*	0.374	8	752.6	8.57	0.174	–0.450	34	203.2	17	1.52E-05	3.0423	578.4
Porkfish *Anisotremus virginicus*	—	—	—	—	—	—	25	203.2	—	1.01E-05	3.1674	—
Sailors Choice *Haemulon parrai*	0.428	7	400.2	1.24	0.220	–0.355	12	203.2	35	2.02E-05	2.9932	320.1
Smallmouth Grunt *Haemulon chrysargyreum*	—	—	—	—	—	—	24	203.2	—	2.77E-03	2.1567	—
Spanish Grunt *Haemulon macrostomum*	—	—	—	—	—	—	39	203.2	—	2.28E-05	3.0295	—
Striped Grunt *Haemulon striatum*	—	—	—	—	—	—	21	203.2	—	1.39E-05	3.0988	—
Tomtate *Haemulon aurolineatum*	0.333	9	441.6	1.89	0.091	–2.095	24	203.2	57	6.19E-06	3.2077	279.9
White Grunt *Haemulon plumieri*	0.375	8	511.9	3.06	0.186	–0.776	18	203.2	24	8.35E-06	3.1612	410.3
Great Barracuda *Sphyraena barracuda*	0.200	15	1238.3	14.03	0.172	–0.461	36	619.2	44	4.11E-06	3.0825	1151.5

Management analyses

We also conducted a multispecies stock assessment and management analysis with the estimates of fishing mortality to examine if current exploitation levels are commensurate with sustainable fisheries. Although 46 exploited reef fish species had been seen or captured in the visual and headboat surveys, only 35 species had population dynamics parameter sets sufficient to conduct a management analysis (Table 3). We noted striking similarities in key relations within taxa as shown by the somewhat discrete clusters of taxa when maximum size dependent on maximum age for a variety of species was plotted (Fig. 5). Mean F estimates for visual survey and headboat data were used to encompass conservatively the range of feasible fishing mortality rates experienced in the fishery over the last two decades. A comparison of methods and data sources also allowed us to consider risks associated with the overall uncertainty bounds for each stock assessment. Results of an example assessment analysis is shown for gray snapper in which

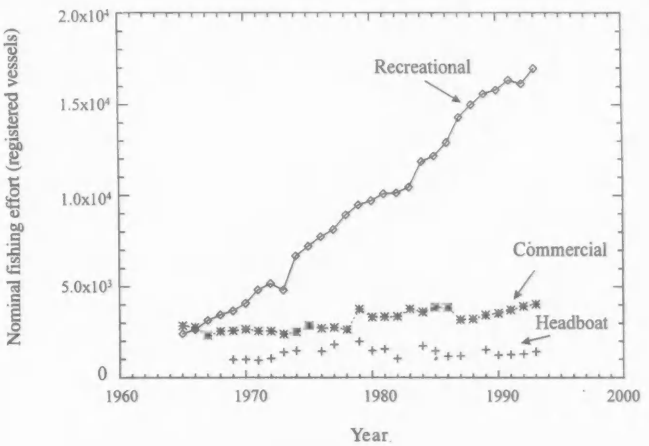

Figure 3

Time series of three types of nominal fishing effort directed at Florida Keys reef fish from 1965 to 1993 based on numbers of recreational (□) and commercial (✱) vessels registered in Monroe County, Florida. Headboats (+) are considered to be a subset of the commercial fishing fleet.

management endpoints like yield-per-recruit (YPR) and spawning potential ratio (SPR) are provided (Fig. 6). These results are typical of the management information provided for each species.

Our analyses indicated that the average size in the exploitable phase for many economically important reef fish populations was marginally above the minimum size of capture regulated by fishery management agencies (i.e. South Atlantic Fishery Management Council and the Florida Marine Fisheries Commission). To assess the impact of these mortality rates on the stock production, we performed an analytical yield analysis to estimate the YPR for each stock, and evaluated the current YPR status in relation to "eumetric" (cf. Beverton and Holt, 1957) or well-balanced fishing in terms of the minimum size of fish captured and level of fishing effort (Fig. 6A). An issue of paramount concern in assessing analytical yield models are the settings of the two dynamic control variables, F and L' (Fig. 6A). From the perspective of optimal decision making, any transition of the fishery over the yield surface should minimize negative risks, while maximizing the economic, ecological, social, and aesthetic aspects. The YPR analysis for gray snapper suggests that the current size (or age) of first capture, L' at 254 mm (=10 in), likely results in "growth overfishing." To maximize the YPR for the range of F operating in the fishery for the last two decades, L' should be increased to greater than 350 mm (Fig. 6B).

Figure 6C shows progressive reductions of gray snapper stock biomass when F is increased to the estimate's lower bound shown in Figure 6B. The likelihood range of $\hat{F}$ (i.e. $\hat{F}$=[0.5,1.1]) is likely also contributing to a very low SPR for gray snapper. In fact, it is below the Federal minimum of 30% SPR (Fig. 6D). The minimum estimated F still reduces SPR to about 29% of the unexploited state, whereas the upper bound estimate results in 15% SPR. The majority of the range of estimated F suggest that the gray snapper stock is also "recruitment overfished" as reflected by reduced spawning potential.

The summary of the SPRs for Florida Keys reef fish (Fig. 7) shows that a total of 13 of 16 groupers, 7 of 13 snappers, and 2 of 5 grunts, for which there are data, are below the SPR that constitutes overfishing by Federal definitions. Overall, 63% of the 35 stocks that could be analyzed were overfished. Linear regressions of SPR on exvessel price showed a significantly negative ($F_{1,14}$=7.55, P=0.0157) slope for grouper and a marginally significant ($F_{1,11}$=4.77, P= 0.0514) negative slope for snapper (Fig. 8).

Discussion

Fishery dynamics

Our results indicate that Florida Keys reef fish populations have been heavily fished for at least the last

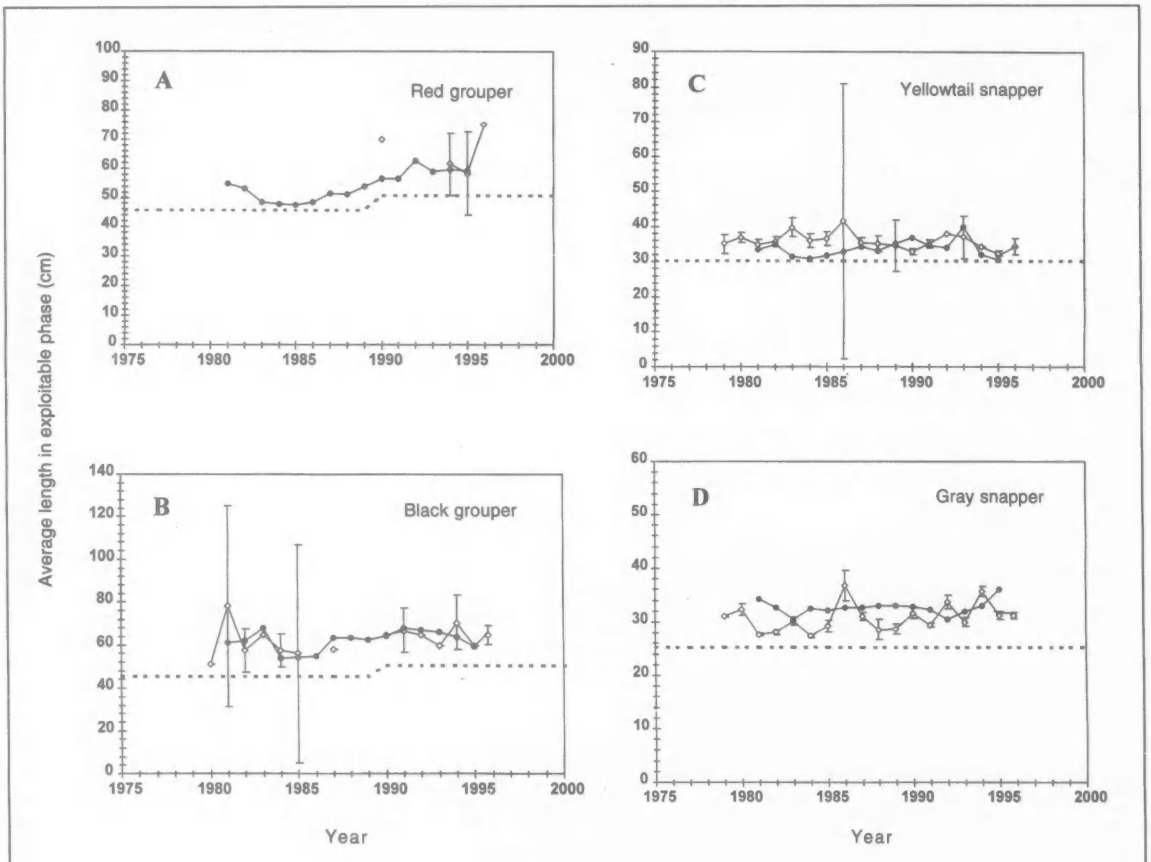

Figure 4

Average length (cm) in the exploitable phase of the stock estimated from headboat (●) and visual survey (○) data for several reef fish stocks during the period 1979 to 1996: (**A**) red grouper, (**B**) black grouper, (**C**) yellowtail snapper, (**D**) gray snapper, (**E**) white grunt, (**F**) bluestriped grunt, (**G**) hogfish, and (**H**) great barracuda. Bars around visual survey estimates are 95% confidence intervals of the mean. Horizontal dotted lines show the minimum size at first capture L' regulated by regional fishery management.

two decades. Total fishing effort has increased substantially because of greater average fishing power per vessel and a much larger recreational fishery. Mace (1997) estimated that the average "fishing power" per vessel (i.e. the average proportion of the stock removed per unit of fishing effort) has increased 4-fold over the previous 25 years mainly because of improved technology involving better vessel designs, hydroacoustics, hydraulics, and navigation (GPS, Loran C, charts). The arithmetic increase of recreational fishing vessels is an important factor also, although its absolute effect on reef fish stocks is unknown because the recreational fleet is distributed diffusely and heterogeneously and has not been well sampled to date.

Stock assessment indicator variable

The estimated average lengths (size) of reef fish in the exploitable phase, determined from statistically independent visual and headboat data, were highly comparable for groupers, snappers, and grunts, supporting their use in the multispecies assessment. Average sizes of hogfish and barracuda, however, differed between the two data sets. The larger average hogfish size in headboat samples appears to be the result of life history patterns and different responses to fishing gears with depth. Hogfish tend to move from shallow to deeper water with age (Davis, 1976) and are more vulnerable to spearfishing than hook-and-line gear. Divers, however, are effectively

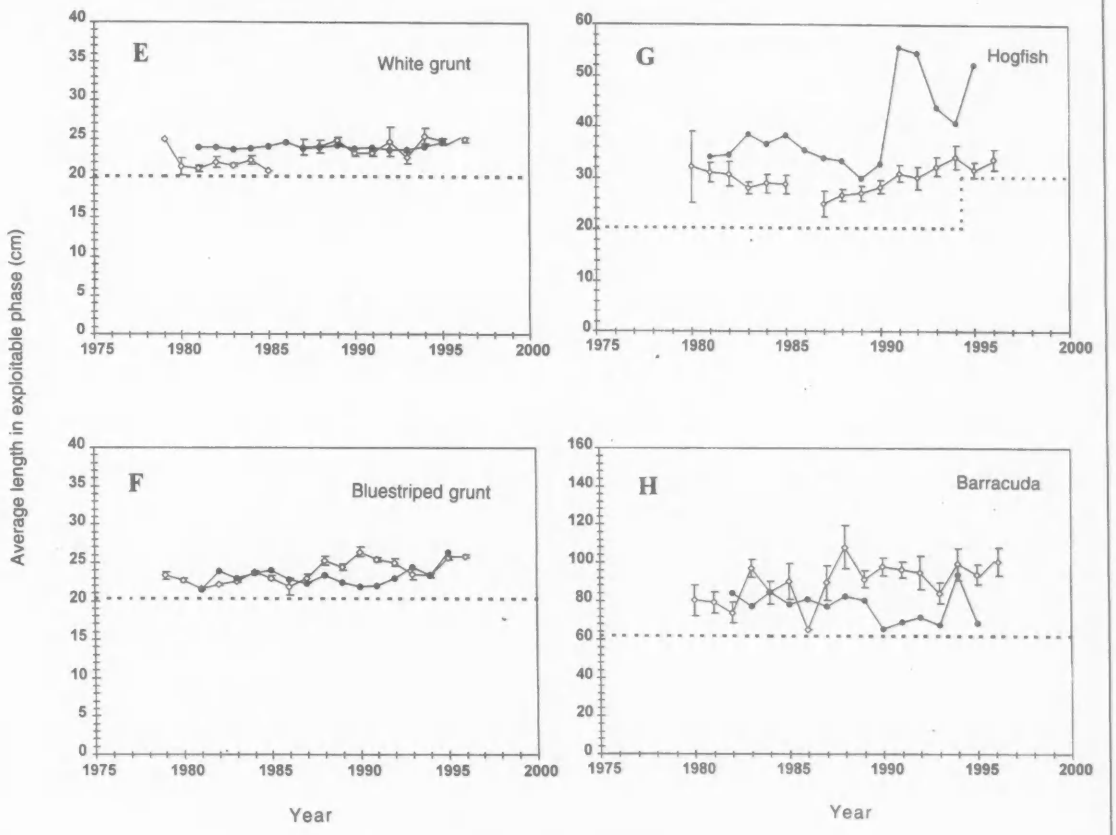

Figure 4 (continued)

restricted to shallower depths for safety reasons. Thus, large hogfish that inhabit depths below safe diving limits are available to only the headboat fleet. In shallow water, divers are more likely to see small hogfish because they are more abundant and because large hogfish are more likely to be selectively depleted by spearfishing. The increased average size in both data sets since the mid-1980s (Fig. 4G) is most likely the result of increased spearfishing regulation, imposed recreational bag limits, and initiation of minimum size limits.

The average size of barracuda diverged in visual samples and headboat landings since the early 1980s (Fig. 4H). This pattern is likely the result of the promotion and expansion of catch-and-release fishing for barracuda during that time period. Decreased fishing mortality resulting from more released barracuda would increase the average size of fish in the exploitable phase and be detected in visual samples. Headboat landings, however, could trend toward smaller fish because more large barracuda increase the frequency of angler "breakoffs" (i.e. fish biting through lines or leaders) and the proportion of releases because only small barracuda are normally retained for human consumption. Large barracuda are avoided because they carry greater risk of ciguatera poisoning, which can result in convulsions and death for humans (de Sylva, 1994).

The trend in average size for grouper, snapper, and grunt stocks was relatively flat over the past 18 years and close to the minimum exploitable length (Fig. 4). The flatness is explained by considering expected $\bar{L}$ from a modeled range of F in an analytical model, given knowledge about current values of $\hat{F}$. The slope of $\bar{L}$ on F was very shallow in the range of the analytical model (Fig. 9), corroborating the empirical estimates in Figure 4. Some stocks appear to have been chronically overfished since the late 1970s. We

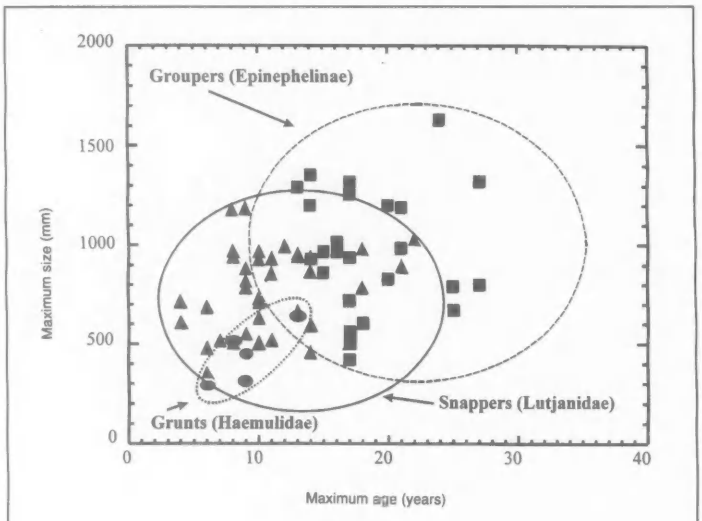

Figure 5

Relationship between the population dynamic parameters maximum size L_λ and maximum age t_λ for three economically important Florida Keys reef fish taxa: groupers, Epinephelinae (■); snappers, Lutjanidae (▲); and grunts, Haemulidae (●).

also noted similarities in key relations within various taxa that separated out into somewhat discrete clusters when maximum size versus maximum age by species is plotted (Fig. 5). This pattern of species clusters suggests that species within the various taxa groupings will likely respond to exploitation in a similar manner. The sensitivity to exploitation is highest for groupers, followed by snappers, and then grunts.

Overfishing and community shifts

Despite conservative assumptions, the estimated fishery exploitation rates suggest that many Florida Keys reef fish stocks are overfished according to definitions for U.S. fisheries (Rosenberg et al., 1996) (Figs. 7 and 9). Many desirable grouper and snapper stocks have low spawning potential ratios (SPRs). Inverse relationships between increased fishing effort (particularly by the recreational sector) (Fig. 3) and the long-term decreased average size and stock biomass (e.g. Fig. 6C) of the most desirable species (e.g. groupers and snappers) are particular concerns.

The Florida Keys reef fishery shows the classic pattern of serial overfishing, in which the more vulnerable species are progressively depleted (Munro and Williams, 1985; Russ and Alcala, 1989). The longest-lived, latest-maturing, and lowest mortality (M) stocks [i.e. groupers] are those first to experience significant declines in population biomass, followed in sequence by intermediate-lived stocks [snappers], and finally by short-lived stocks [grunts] [Fig. 7]). Within families, the inverse relations between the spawning potential ratio and exvessel market price (Fig. 8) are consistent with serial overfishing. As expected, the most valuable snapper and grouper also tend to have the lowest spawning potentials. During the time frame of this study, numerous measures were taken to reduce fishing mortality in state and federal waters. Fish traps were progressively eliminated between 1980 and 1992, and numerous bag limits and minimum size limits were imposed. Fisheries were closed for queen conch (*Strombus gigas*), jewfish (*Epinephelus itajara*), and Nassau grouper (*E. striatus*). These actions are evidence of trends reported in this study.

Our data suggest that there may have been substantial changes in the composition of the biomass and abundance of the reef fish community over the past several decades. Although many groupers and snappers have declined, apparently in response to growing fishing effort, some grunts have increased in relative abundance. Claro (1991) noted a similar process in the Golfo de Batabano, Cuba, and hypothesized that chronic overharvesting of snappers resulted in shifts in community composition in favor

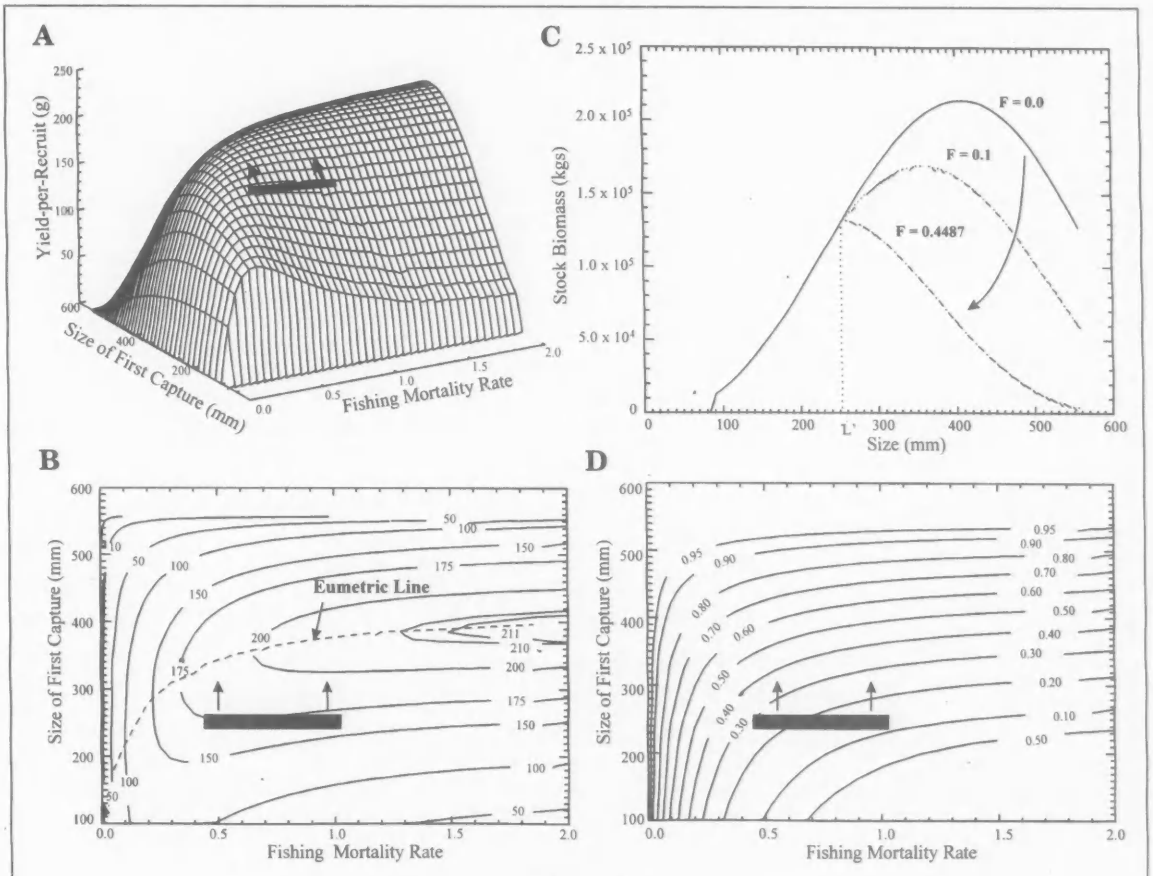

Figure 6

Example calculation of an analytical yield model management analysis for gray snapper: (**A**) 3-dimensional yield-per-recruit YPR surface (g) as a function of the fishing mortality rate F (per yr) and size at first capture L' (mm); (**B**) YPR isopleths in lifetime yield-per-recruit; (**C**) stock biomass dependent on size for several exploitation levels; and (**D**) spawning potential ratio (SPR) as a function of F and L'. REEFS model input parameter values are from Table 3. Shaded rectangles in panels A, B, and D show estimated range of F and L'. Darkened rectangle in panel D indicates the range of F estimates that exceed the Federal 30% SPR overfishing definition following Rosenberg et al. (1996).

of grunts. Another indication of significant change was the explosive growth of barracuda (Fig. 4H) which may be explained by several factors. First, there is little directed commercial or recreational fishing for barracuda as food because of health concerns. Second, growth of catch-and-release fishing by sport anglers and reduced emphasis on spearfishing may have substantially lowered barracuda mortality. Third, other top predators, such as groupers, snappers, and sharks, have been intensively fished, therefore probably lowering competition for food, while, at the same time, barracuda still retain a large and possibly increasing prey base of grunts and other small fishes. Increased abundance and biomass of a top predator like barracuda could be a management concern if barracuda substantially impact reef fish community dynamics. For example, excessive predation on popular sport fishes like snappers could counteract potential reductions in fishing mortality sought by traditional management.

An adjustment of minimum sizes of first capture (L') and fishing mortality rates (F) may mitigate the apparent growth and recruitment overfishing conditions in the fishery. This adjustment should be done in a multispecies context to optimize the biotic and fishery potential of the reef fish assemblage. However, traditional management actions alone are unlikely to be sufficient because they can be circum-

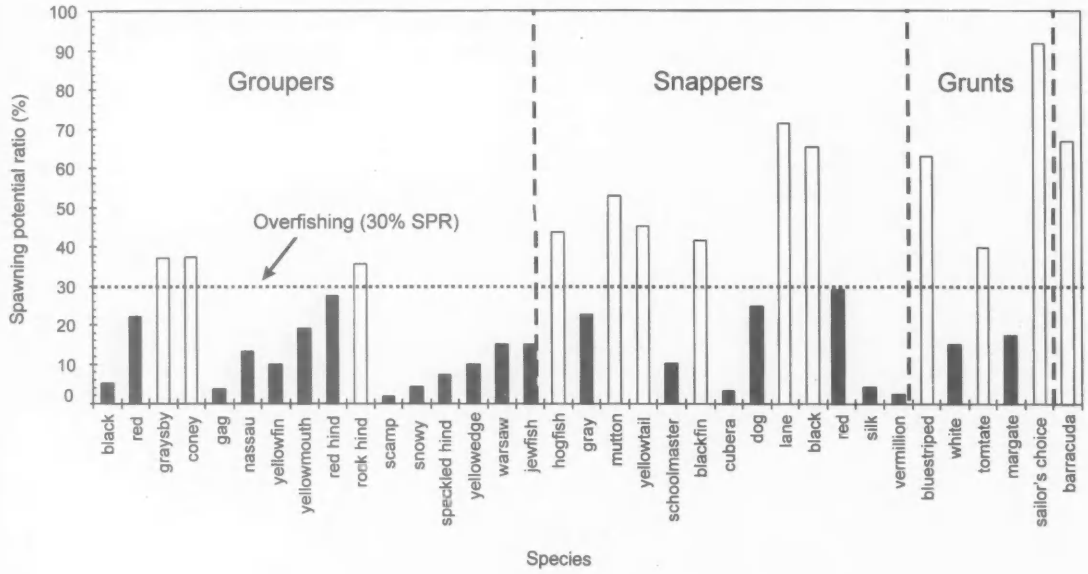

Figure 7

Estimates of percent spawning potential ratio (SPR%) for 35 species of Florida Keys reef fish comprise groupers, snappers, grunts, hogfish, and great barracuda. Darkened bars indicate stock "overfishing," and open bars indicate the stock is above the 30% SPR U.S. Federal standard.

vented and habitually fail to control fishing effort effectively, particularly in an open access fishery (Waters, 1991; Bohnsack and Ault, 1996). For example, bycatch mortality and high fishing effort from the expanding fleets can make size limits ineffective. In theory, every fish can be caught once it reaches minimum legal size with the result that insufficient mature adults survive to reproduce. The tradition of open-access management systems coupled with risk-prone management decisions remains a principal obstacle to achieving renewable resource sustainability (Rosenberg et al., 1993).

Reversing adverse trends in the Keys reef fishery are likely to require other innovative approaches for controlling exploitation rates. Rothschild et al. (1996) recommended that fishery management maintain a systems view of the resources, emphasizing strategy over tactics. With this in mind, we recommend coupling traditional management measures with a spatial network of areal closures called "no take" marine reserves. Marine reserves provide an ecosystem management strategy for achieving long-term goals of protecting biodiversity while maintaining sustainable fisheries. The establishment of a network of small (16 to 3,000 ha) no-take reserves in the FKNMS on 1 July 1997 (U.S. Dep. Commerce, 1996) is a first step. A key to the success of this effort is a conscientious, continuous assessment program for integrating fishery-independent and fishery-dependent data to evaluate the effectiveness of these reserves (Bohnsack and Ault, 1996). With adaptive management (Walters, 1986), improvements can be implemented over time.

Multispecies assessment

Our overall goal was to improve the scientific basis for managing tropical multispecies fisheries by providing an efficient, quantitative framework to assess multispecies fisheries. New assessment methods are particularly needed for complex fisheries that have been poorly documented, are not well understood, and face increased exploitation. Traditional single-species stock assessment methods are at times inappropriate or inadequate to deal with the dynamics and structure of multispecies assemblages with large numbers of exploited species (Caddy, 1981; Ault and Fox, 1990; Appledorn, 1996). Owing to a lack of data and basic biological information, only a few reef species in the entire southeastern U.S. have had comprehensive stock assessments.

We emphasized a multispecies ecosystem approach because traditional fishery models have been ineffectual in creating sustainable fisheries (Ludwig et al., 1993; Sharp, 1995; Caddy, 1996; Russ, 1996).

Single-species fishery management models built to maximize fishery yield and economic rent ignore critical biological and physical interactions and cumulative stresses on habitats. Reef fish stocks are likely to be regulated by trophic interactions at the individual, population, and community levels. Also, application of "traditional" fishery management models developed for temperate species to tropical coral reef assemblages is tenuous. In response to these problems, the National Research Council Committee on Fisheries (1994) recommended developing multispecies ecosystem management programs for building sustainable fisheries. Successful implementation of such programs will require innovative research, new management strategies, less destructive and wasteful fishing methods, protection of critical and sensitive habitats, and more effective education.

Our retrospective analysis emphasized fishery-independent data. Although fishery-independent assessments can provide reliable measures of fish abundance, population dynamics, and community composition (Gunderson, 1993), their application in multispecies fishery assessments have been limited. We predict an increasing need to rely on such data for assessment purposes because fishery-dependent data will become less available and less useful as new regulations are imposed that will establish larger size limits, closed seasons, closed fishing areas, and species prohibited from being fished. Also, the shifting emphasis from commercial to recreational fishing makes collecting fishery-dependent data much more difficult and expensive.

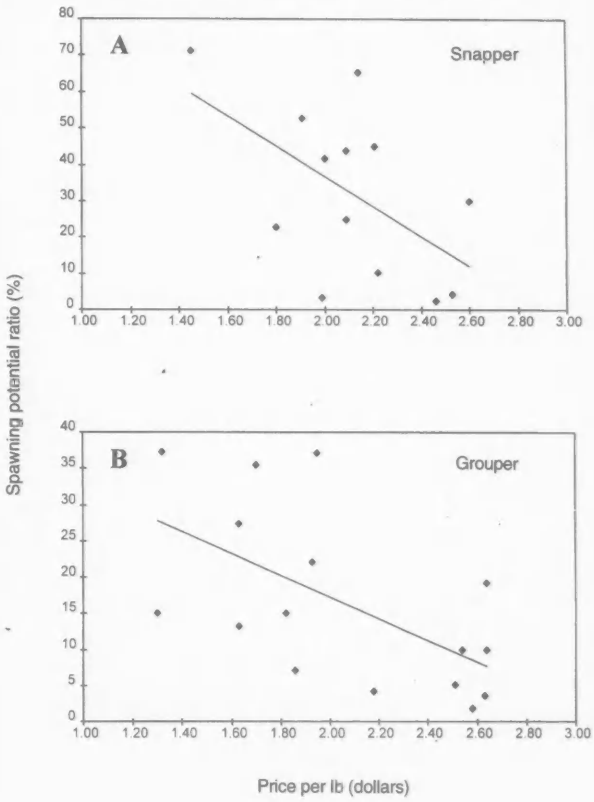

Figure 8

Linear regressions of estimated species spawning potential ratio (y) on average 1996 Monroe County exvessel price (x) for: (**A**) snapper: $y = 119.59 - 41.38x$; and, (**B**) grouper: $y = 47.35 - 15.03x$.

Results from this 18-year retrospective assessment are encouraging in providing estimates of stock status. However, several assumptions that simplify the population dynamics of the various species make it prudent to consider population estimates first-order approximations. The error intrinsic in population-rate estimates derived from surveys depends on the accuracy and precision of the basic survey. Errors ultimately propagate upwards during a series of calculations used to determine the average size, total mortality rates, fishing mortality rates, yield-per-recruit, and finally the spawning potential ratio, which is the current focus of management decisions. Also, although the Florida Keys fishery represents a major fishing area, it does not necessarily represent the entire stock range for an individual species. It is possible that mature stock components exist outside the fishing area.

Six actions could improve future assessments. First, develop suitably structured spatial models for linkages between habitat use and fish ontogeny to "fill-in" the map of population estimates for areas not sampled. Second, calibrate the relative statistical power of diver surveys and headboat fishing gear. Ideally, diver observations should relate to what fishermen catch. Because the fishing mortality rate of headboats (and viewing power of divers) are considered strictly proportional to average population abundance, we must understand the fraction of the stock assessed per unit of effort and the interrelationship of the efficiency of the two "gear" types. Third, increase temporal and spatial sampling coverage to increase survey precision and resolution. Fourth, tune fishery-independent surveys with other indices of stock abundance. In this retrospective analyses, no attempt had been made to have the two survey

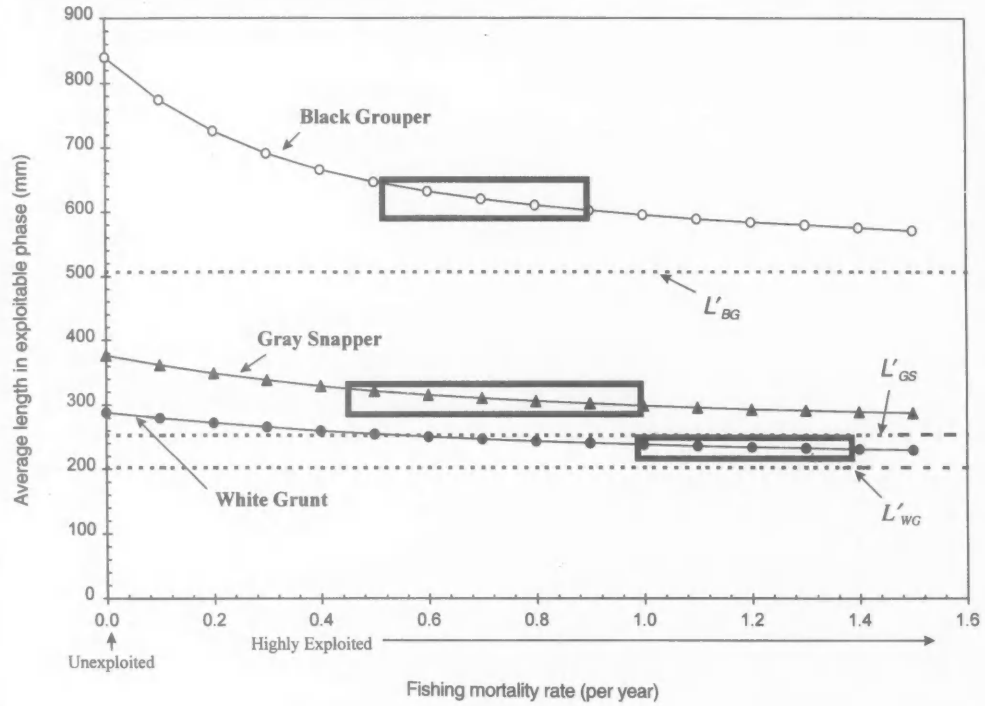

Figure 9

Simulation of equilibrium relationship of average length in the exploitable phase $\bar{L}$ dependent on fishing mortality rate F using the REEFS model for several reef fish taxa: (**A**) black grouper (○); (**B**) gray snapper (▲); and (**C**) white grunt (●). Boxes around species curves show the range of F estimates from the retrospective analyses.

types coincide with respect to sampling effort or locations within the Florida Keys. Fifth, employ new sampling technologies, such as hydroacoustics, green band lasers, and stereo video cameras to improve the accuracy and cost effectiveness of biomass and abundance estimates. Sixth, improve basic biological information on growth, reproduction, mortality, feeding, and recruitment, which are fundamental elements of stock assessment. The models and conclusions presented here are strongly influenced by the accuracy of the parameter estimates and the source for these estimates is not always reliable.

Conclusions

We used a new approach involving fishery-independent data to conduct a quantitative retrospective multispecies assessment of changes in the Florida Keys multispecies reef fish community. Our results show that fishing effort and mortality levels are very intense, that many stocks are "overfished," and that exploitation has likely altered the structure and dynamics of the reef fish community. Inevitable increases in fishing effort, particularly by recreational anglers, combined with habitat degradation by rapid growth of human populations in the region, if unabated, will increase the potential for overfishing and ecosystem changes. Without effective intervention by regional fishery management to bring fishing effort under control, reef fish stocks will likely continue to decline. A spatial network of "no take" marine reserves, combined with traditional management measures, have the potential to reverse these trends for many species and to allow the long-term goals of building sustainable fisheries and protecting biodiversity to be achieved.

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Reproductive patterns, sex ratio, and fecundity in gag, *Mycteroperca microlepis* (Serranidae), a protogynous grouper from the northeastern Gulf of Mexico

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Abstract.—We determined sex ratio, spawning season, batch fecundity, spawning frequency, and annual fecundity for gag (Serranidae: *Mycteroperca microlepis*), a protogynous hermaphrodite. Gag were randomly sampled from 1991 through 1993 (n=1398) and selectively sampled with a bias towards heavily pigmented fish in 1994 (n=648). All samples were taken from commercial and recreational fisheries in the northeastern Gulf of Mexico. Sex ratio was 49 females:1 male for the 1991–93 samples. Heavily pigmented gag (n=62), commonly thought to be males, were collected from waters >41.0 m during all months except January and March. Of these, 60 were histologically sexed and found to be 5.0% female, 3.3% possibly early transitional male, and 91.7% male. Indeterminate spawning generally occurred from February through April in water depths >30.5 m. Hydrated oocytes were homogeneously distributed in hydrated ovaries. Shortest length and youngest age at spawning were 577 mm total length (TL) and 3 years for females, and 981 mm TL and 8 years for males. The highest batch fecundity (865,295 hydrated oocytes) occurred in an 8-year-old, 1038-mm-TL gag. Batch fecundity had a significant (α=0.01) positive correlation with TL, gutted body weight, and age but was most strongly correlated with TL. Average annual spawning frequency ranged from 8 to 27 for 2- to 9-year-old fish, varying significantly by year (P<0.05) and among years and age classes (P<0.02). Annual fecundity estimates ranged from 0.065 to 61.4 million and correlated well with age.

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Fishery Bulletin 96:415–427 (1998).

The spawning potential ratio (SPR), which is used to estimate the adult stock size as a percentage of the unfished stock, is an important assessment tool in the management of fish stocks (Goodyear, 1993). An accurate determination of SPR requires a basic understanding of reproduction (Huntsman and Schaaf, 1994), including information on sex ratio, spawning season duration, and size (and age) at first spawning, as well as estimates of batch fecundity, spawning frequency, and annual fecundity by fish size.

Gag (Serranidae: *Mycteroperca microlepis*), a large, economically important, shallow-water grouper found from Massachusetts to Rio de Janeiro, Brazil, (Briggs, 1958) is heavily fished in the Gulf of Mexico on Florida's western shelf, with 1986–92 annual commercial landings of about 6.80×10^5 kg (1.5 million lb) and recreational landings of 0.2–0.6 million fish (Gulf of Mexico Fishery Management Council[1]; Schirripa and Goodyear[2]). The gag is a winter-spring spawning, monandric protogynous hermaphrodite that matures sexually around 550 mm total length and 3 to 6 yr (McErlean and Smith, 1964; Collins et al., 1987; Bullock and Smith, 1991; Hood and Schlieder, 1992; Coleman et al., 1996; Koenig et al., 1996). Gilmore and Jones (1992), who described the reproductive behavior and color variation of gag off the east coast of Florida, assumed that large gag with heavy pigmentation ("black-belly" and "black-back") were males. Similarly, Bullock and Smith (1991) assumed that large gag "with dark pigmentation ventrally" from the Gulf of Mexico were male. More recently, Koenig et al. (1996) and Coleman et al. (1996) have described reproductive styles of gag and the apparent effects of fishing on gag spawning aggregations.

Although these studies (above) have examined some aspects of gag reproduction, few have addressed

[1] Gulf of Mexico Fishery Management Council. 1989. Amendment number 1 to the reef fish fishery management plan. GMFMC, Tampa, Florida, 356 p.

[2] Schirripa, M. J., and C. P. Goodyear. 1994. Status of the gag stocks of the Gulf of Mexico: assessment 1.0. Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Drive, Miami, FL 33149.

either fecundity or spawning frequency, and none have used the methods developed by Hunter et al. (1985) for multiple-spawning fishes. Hunter's methods have been used successfully to estimate batch fecundity, spawning frequency, and annual fecundity in other Gulf of Mexico fishes similar to gag in size and longevity (e.g. Fitzhugh et al., 1988; Taylor and Murphy, 1992; Render and Wilson, 1992; Fitzhugh et al., 1993; Nieland and Wilson, 1993; Wilson and Nieland, 1994; and Collins et al., 1996). Such estimates obtained with these newer methods are far more accurate than the previously used "ovarian egg number" methods for multiple spawning fishes (as described in Hunter et al., 1985).

In this study, we estimate sex ratio, spawning season duration, length and age at first spawning, depth of spawning, batch fecundity, spawning frequency by year, spawning frequency by size and age, and annual fecundity in gag from the Gulf of Mexico. We also test the assumption that heavily pigmented gag represent only males using histological examination of gonads of heavily pigmented fish.

Methods

Gag were randomly sampled from commercial and recreational landings from Panama City to St. Petersburg, Florida, in 1991, 1992, and 1993. In 1994, we asked commercial fishermen to leave all heavily pigmented gag ungutted so that they could be examined for sex. Gag were considered heavily pigmented only if they retained the heavy-black pigment on the ventral portion of the abdomen after death (e.g. plate XVI, Fig. D., page 237, in Bullock and Smith, 1991). Total length (TL, in mm), fork length (FL, in mm), and total (ungutted) weight (TW, in g) were recorded before removing gonads, which were kept on ice prior to examination.

Gonads of reproductively active gag are so large that they require subsampling for determination of sex. To ensure that a single tissue sample per female would be adequate to estimate maximum oocyte diameter and hydrated oocyte counts, we first tested for tissue homogeneity. To test for homogeneity of oocyte diameter, three bilobed ovaries with hydrated oocytes were divided into six equal sections (three from each lobe) and subsampled to determine the frequency distributions of oocyte diameters; they were tested for homogeneity with a Kolmogorov-Smirnov two-sample test (Sokal and Rohlf, 1981). To test for homogeneity of density of hydrated oocytes, we used six hydrated ovaries divided in the same manner and determined the number of hydrated oocytes per gram; samples were tested for homogeneity with a two-way ANOVA (SAS, 1988).

We made a preliminary determination of sex in gag using fresh, unstained samples. A small sample was removed from each gonad, teased apart, and viewed microscopically (250×). Sex was assigned according to the following criteria: females had oocytes and no tissues that could be mistaken for spermatogenic tissue; males had no oocytes (or few small oocyte remnants); and transitional males had high numbers of oocytes and possible sperm (Shapiro et al., 1993).

Female gonads were then microscopically staged. Maximum oocyte diameter (MOD) was recorded; the most advanced oocyte type present was noted and used to assign individuals to one of five ovarian-maturation stages: 1) mature, resting (MOD<0.12 mm and clear); 2) early developing (MOD<0.20 mm and slightly opaque); 3) late developing (MOD=0.20 to 0.59 mm and opaque); 4) ripe (MOD>0.59 mm and mostly transparent); and 5) spent (much loose particulate matter in flaccid ovary) (West, 1990). After fat and mesentery were removed, gonads were blotted dry, weighed to the nearest 0.1 g., and placed in 10% buffered formaldehyde solution.

We then selected and prepared some of the gonad samples (above) to verify sex and stage using standard histological techniques. Five-µm-thick sections were prepared from tissues embedded in paraffin and stained with Harris's hematoxylin and eosin. Ovarian stages were assigned on the basis of the most advanced oocyte or follicle stage present: 1) primary growth; 2) cortical alveolar; 3) vitellogenic; 4) hydrated; and 5) spent (presence of postovulatory follicles [POFs]). Stages 1–4 followed Wallace and Selman (1981). Histological stages of possible early transitional males and functional males were as follows: 6) possible early transitional males had active female tissue with possible crypts containing primary spermatocytes (Moe, 1969; Johnson, 1995); 7) mature inactive males had a few secondary spermatocytes and remnant oocytes (primary growth and atretic only); 8) mature active males had many secondary spermatocytes and remnant oocytes; 9) ripening males had spermatids in ducts; and 10) ripe males had tailed spermatozoa in ducts. Sex and stage were compared by gonad-region for all heavily pigmented gag. Physical condition of the gonad (e.g. intactness, presence of parasites, possible preservation problems) was also noted.

We estimated duration of the spawning season by using two techniques: 1) plotting gonadosomatic index (GSI=gonad weight (100)/TW) by month for all gag with gonads in good condition (≥90% intact) and 2) determining when hydrated ovaries with nondegenerated POFs appeared. Proof of actual spawning (and not just the presence of "ripe" ovaries, as discussed in Sadovy et al., 1994) was provided by

POFs. Size and age at first spawning, and water depth of spawning, were determined with only histological stage-4 females and stage-10 males. Depth of spawning was indicated by depth of catch, as determined from interviews with fishermen.

Batch fecundity estimates involved counting whole, hydrated oocytes taken from cross sections of gonads and weighed (to the nearest 0.001 g) following Hunter et al. (1985). Samples were examined histologically for the presence of POFs and hydrated oocytes. The POFs in samples were noted as 0 (absent), 1 (degenerating), or 2 (nondegenerating) (Fitzhugh and Hettler, 1995). Ovaries with nondegenerating POFs were omitted from batch fecundity estimates to avoid biases in determining the number of hydrated oocytes per gram of tissue (Hunter et al., 1985). Batch fecundity estimates were calculated by dividing the product of gonad weight and number of hydrated oocytes by the sample weight. Any fish collected late in the spawning season were omitted from batch fecundity analyses because of apparent decreases in batch size (e.g. Fitzhugh et al., 1988).

Spawning frequency (the number of spawnings per year by a female) was estimated by dividing the duration of the spawning season by the average number of days between spawning for all females (Hunter and Macewicz, 1985; Hunter et al., 1986). Duration of the spawning season was the number of days between the first and last occurrence of hydrated oocytes or POFs each year. The average number of days between spawning for all females (> or = TL of the smallest hydrated fish) was 100% divided by the percentage frequency of hydrated females. For example, if the spawning season was 100 days long and females spawned every two days (with 50% hydrated), then spawning frequency would be 50.

We obtained annual fecundity estimates by multiplying batch fecundity by spawning frequency. Age-dependent spawning frequency was estimated with stage-4 females within each age group. Because spawning frequency varied by age and year, these variables were considered separately in calculating annual fecundity. We analyzed the following relationships using regression: batch fecundity (BF) × TL, $BF \times age$, and $BF \times$ *gutted body weight* (*GBW=total weight – gonad weight* = $TW - GW$); *spawning frequency* × *age*; *annual fecundity* (AF) × TL, $AF \times age$, and $AF \times GBW$.

Most fish were aged by using whole or sectioned sagittal otoliths (Johnson et al., 1993). Whole otoliths were adequate for ageing smaller fish (<900 mm TL). We sectioned otoliths for larger gag (>899 mm TL) to facilitate reading outer rings.

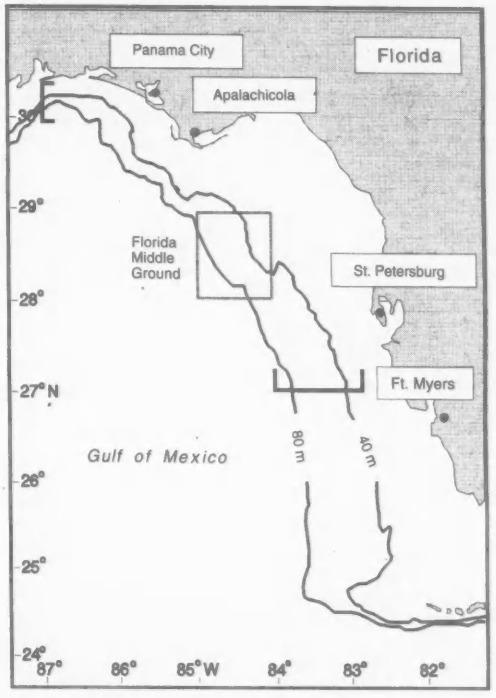

Figure 1

Area sampled for gag from commercial and recreational catches, 1991–94. Total area sampled, along the 40–80 m contour, is encompassed by brackets; most samples were collected from gag caught in the area south of Panama City to the Florida Middle Ground (the latter is indicated by the box).

Results

Of all the gag collected from February 1991 through December 1994 (n=2,046), most (61.7%) were taken from February through May between Panama City and the Florida Middle Ground (Fig. 1). A few samples were collected from off Pensacola, St. Petersburg, and Ft. Myers, FL. The majority of commercial and recreational landings were <24 h old when sampled. Depth data recorded with samples were predominately from commercial catches (57.2%). Commercial catches were usually from greater water depths (mean=57.2 m, n=697) than those for recreational catches (mean=32.6 m, n=73). Most 1991 samples (n=463) were from the commercial fishery (78.1%). Most 1992 samples (n=318) were from the recreational fishery (85.5%). Samples in 1993 (n=617) came from each of the fisheries in approximately equal numbers (commercial =49%). Most 1994 samples (n=648) were from the commercial fishery (68.6%).

Because neither oocyte diameter-frequency distributions for oocytes >0.08 mm in diameter (α=0.05; Kolmogorov-Smirnov two-sample test; $d_{0.05}$=0.1103;

Table 1

Effect of location of gag tissue samples on hydrated oocyte counts per unit of weight (g). Locations are anterior (1), mid (2), and posterior (3) of ovarian lobes. Analysis of variance indicates significance of location within a lobe for number of hydrated oocytes per gram of tissue. SS = sum of squares; MS = mean square.

Positions of sample in ovary	Lobe 1			Lobe 2			Both lobes		
	$\bar{x}$	SD	n	$\bar{x}$	SD	n	$\bar{x}$	SD	n
1	918	92	6	951	107	6	934	97	12
2	914	81	6	932	180	6	923	133	12
3	875	140	6	931	144	6	903	138	12
Total	902	103	18	938	138	18	920	121	(36)

Source	df	SS	MS	F	$P>F$
Lobe	1	11,460.23	11,460.23	0.74	0.40
Region	1	6018.21	6018.21	0.39	0.54
Interaction	1	803.81	803.81	0.05	0.82
Error	32	496,556.28	15,517.38		
Total	35	514,838.52			

n=5,450 oocytes; range=0.04 to 1.20 mm) nor hydrated oocyte counts per gram (Table 1) differed significantly among ovarian regions, we randomly sampled one region on each ovary to determine maturation stage, maximum oocyte diameter, and fecundity. Gag hydrated ovaries contained a mean of 920 hydrated oocytes per gram of ovarian tissue (range=875 to 951, SD=121, n=6 fish) (Table 1). The distinct clusters of oocytes of various diameters, including stage-1 and stage-2 oocytes, in gag ovaries throughout the spawning season indicated that gag is a multiple and indeterminate spawner.

Gag ovaries were usually much larger than testes (mean ovary weight=46.5 g, mean testes weight= 26.7 g). The largest ovary and testes weighed 1.60 kg and 120.0 g, respectively. Wormlike parasites were common in ovaries. Histological appearance of gag ovaries (nontransitional) was typical for marine teleosts (Wallace and Selman, 1981), except that some functional females appeared to contain crypts of spermatogonia.

An unusual condition observed in three females (stage 1 or 2) was the presence of a 5-mm thick lining (around the inside perimeter of the abdominal cavity) of compressed, hydrated oocytes apparently caused by rupture of the ovarian wall. These three fish were caught after the peak spawning season (May 1994, June 1993, and July 1994). We found no such lining in any of the other specimens examined.

We found that sex determinations and maturation-stage determinations were made with variable accuracy in fresh and histologically prepared samples. The two examinations gave the same results 89% of the time for sex determination but only 70% of the time for stage determination. The main reason for this poor comparison of the two staging techniques was that we could not accurately identify spent females (with POFs) or transitional males from fresh samples, because POFs and sperm could only be positively identified histologically.

Sex ratio

Sex ratio from all random samples (pooling data for 1991–93) was approximately 49 females: 1 male. Our emphasis on collecting gag with dark ventral pigmentation in 1994 clearly increased the overall percentage of males: 52.5% of all males for 1991–94 (n=59) were collected in 1994. Percentage of males was 1.9% in 1991–93 and 4.7% in 1994. Females were collected year round and males were collected in all months but January. Possible early transitional male gag (n=3) were found only during February, April, and May.

Ventral pigmentation

Gag with heavy ventral pigmentation (n=62) were collected in all months but January and March in waters >41 m (Table 2). Sex determination (n=60) showed that 5% were females (Fig. 2A), 3.3% were possible transitional males (Fig. 2, B and C), and 91.7% were males (Fig. 2D). Sex and stage were homogeneous among six gonad regions in all heavily pigmented fish.

Spawning period

Winter-spring spawning, indicated by the presence of hydrated oocytes, was corroborated by GSI (Fig.

Table 2

Results of histology on gonads of gag observed with heavy ventral pigmentation, 1991–94 (M = male, F = female, T = possible early transitional male). Stage (see "Methods" section): 1 = primary growth; 3 = vitellogenic; 4 = hydrated; 6 = possible sperm crypts; 7 = inactive; 8 = active; 9 = ripening; and 10 = ripe. C = commercial and R = recreational. Numbers in parentheses indicate number aged.

Year and month	*n*	Total length (mm)	Age (yr)	Gonad wt.(g)	Catch depth (m)	Fishery	Sex	Stage
1991								
Feb	1	985	—	31.2	—	C	T	6
	1	886	—	15.4	45.7–54.9	C	M	8
May	2	1140,1150	12,14	47.2,69.4	—	C	M	10
Sep	1	1140	—	33.1	—	R	M	10
Dec	1	1170	—	28.9	—	C	M	10
Total	6	886–1170	12,14 (2)	15.4–69.4	45.7–54.9	C,R	T,M	6–10
1992								
Jun	2	1100,1162	8,11	19.2,22.4	—	R	M	8–10
Oct	1	1276	20	8.9	39.6–[1]	R	M	9
Dec	6	965–1143	11 (1)	24.7–58.6	57.9–68.6	C	M	7–10
Total	9	965–1276	8–20	8.9–58.6	57.9–68.6	C,R	M	7–10
1993								
Feb	1	1170	17	84.5	54.9–76.2	C	M	10
	1	858	7	54.6	—	R	F	3
Jun	1	1030	9	55.2	—	R	F	1
Jul	6	1070–1290	10–20	12.8–25.7	57.9–59.4	C,R	M	7–10
Aug	1	1105	11	13.9	54.9–67.1	C	M	9
Oct	2	1065,1095	13,–	13.6,17.9	115.8	C	M	9
Total	12	858–1290	7–20	12.8–84.5	54.9–115.8	C,R	M,F,T	1–10
1994								
Apr	8	980–1201	7–12	35.7–49.9	67.1–109.7	C	M	10
	1	1120	12	267.7	67.1	C	T	6
	1	1090	9	152.6	67.1	C	F	4
May	11	1055–1240	8–22	6.4–120.0	53.3–106.7	C	M	8–10
Jul	4	1130–1210	11–20	12.8–22.7	54.9–99.1	C	M	9–10
Aug	4	1085–1235	—	18.2–27.8	79.2	C	M	9–10
Sep	1	1175	—	40.9	50.3	C	M	10
Oct	1	1242	—	30.9	79.2	R	M	10
Nov	1	1230	—	21.8	—	C	M	10
Dec	1	981	—	5.4	41.1-44.2	C	M	10
Total	33	980–1240	7–22	5.4–267.7	41.1–109.7	C	M,F,T	4–10
Grand total (1991–94)	60	858–1290	7–22	5.4–267.7	41.1–115.8	C,R	M,F,T	1–10

[1] Questionable depth from spearfishing tournament.

3, A and B). Female GSIs (n=1,695) ranged from 0.01 to 8.29, with greatest mean GSI (0.21–2.60) occurring from February through March in all years (Fig. 3A). Male GSIs (n=59) ranged from 0.02 to 0.82, with greatest GSI occurring during February (n=1) in 1991 (Fig. 3B). Possible early transitional male GSI (n=1) was 1.65 in April 1994 (only one possible transitional male with an intact gonad and an accurate total weight was collected).

Histological staging of ovaries collected in 1993 (n=209) and 1994 (n=437) also confirmed winter–spring spawning (Fig. 4). All ovaries were stage 1 from June through September and stage 2 from October through January. Stage-3 ovaries first appeared in December and stage-4 in February. Stage-4 and stage-5 ovaries indicated that spawning occurred from February through April in 1993–94, corroborating GSI analysis. Stage-5 ovaries (containing nondegenerating POFs) were extremely rare (n=7), occurring only in January, March, and July 1993, and April 1994. Small numbers of hydrated oocytes appeared as remnants in the center of stage-1 ovaries after the spawning season.

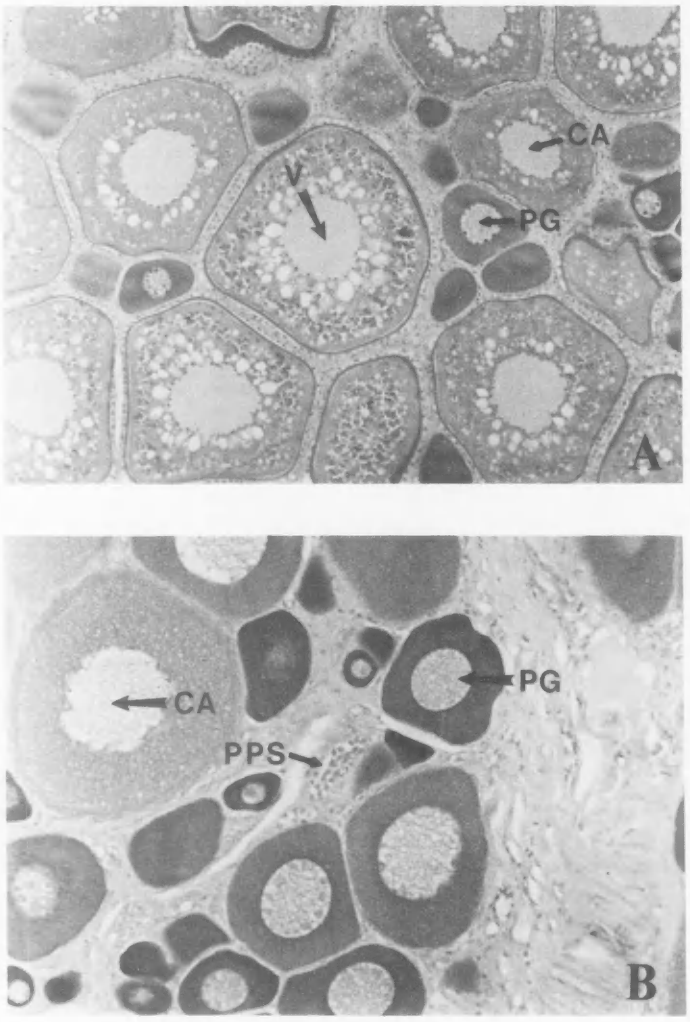

Figure 2

Photomicrographs of histological sections of gag with heavy ventral pigmentation: (**A**) ovarian tissue from an 858-mm-TL female caught in February 1993; (**B**) tissue from a 985-mm-TL possible early transitional male caught in February 1991; (**C**) tissue from a 1120-mm-TL possible early transitional male caught in April 1994; (**D**) testicular tissue with remnant oocytes from a 1143-mm-TL male caught in December 1992; PG = primary growth oocyte; CA = cortical alveolar oocyte; V = early vitellogenic oocyte, EHO = early hydrated oocyte (with coalescing yolk globules); PPS = possible primary spermatocytes; PS = primary spermatocytes; SS = secondary spermatocytes; MS = mature spermatids; and RO = remnant oocyte. Magnification was 132× for A and 264× for B–D.

Spawning mainly occurred from February through April 1991–94, but some evidence of spawning also occurred in December, January, May, June, and July. A total of 173 stage-4 and stage-5 ovaries were found during February, March, and April (n=895). No hydrated ovaries and only one ovary with POFs were found during December (n=58) and during January (n=77). Only one hydrated ovary, one ovary with hy-

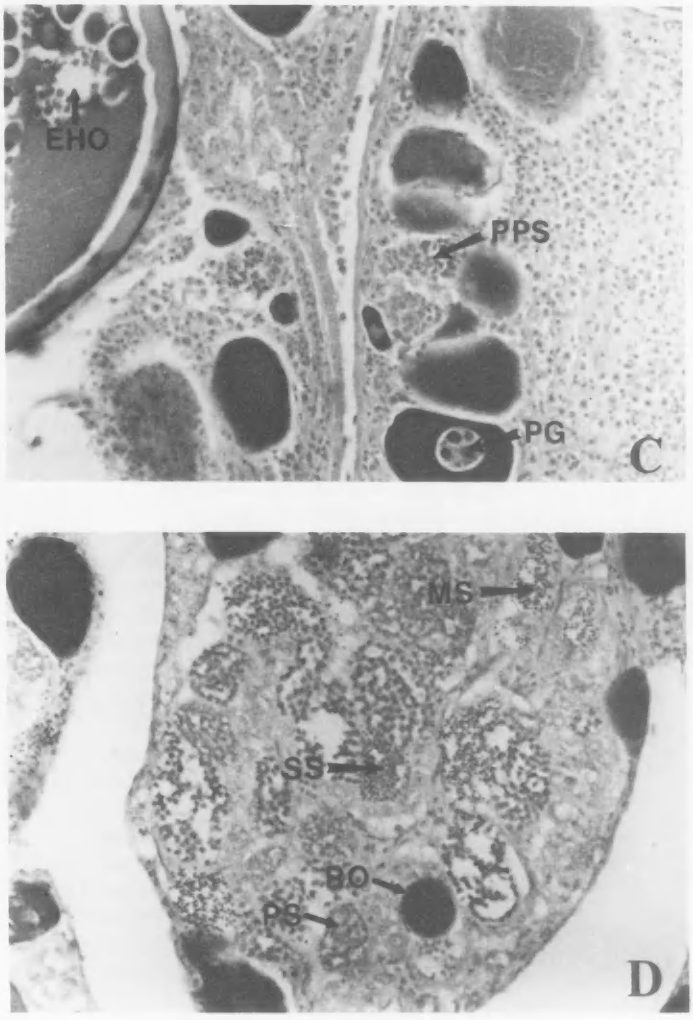

Figure 2 (continued)

drated oocyte remnants, and no ovaries with POFs were found during May (n=306). Hydrated oocyte remnants (in two ovaries) and POFs (in one ovary) were found in June (n=180) and July (n=159).

Length and age at first spawning, and depth of spawning

Length at first spawning (see "Methods" section for definition) was 710 mm TL in 1991, 570 mm TL in 1993, and 670 mm TL in 1994 for females, and 980 mm TL for males in 1994. Age at first spawning was 3 years for females and 7 years for males. Stage-4 females were caught at depths of 30 m and greater. All males were caught at depths greater than 41 m.

Batch fecundity

Batch fecundity estimates (n=39) ranged from 10,864 to 865,295 hydrated oocytes (Fig. 5). These estimates came from gag 690–1065 mm TL, 4.5–16.5 kg TW, 23.4–871.9 g ovary weight, and 3–9 years of age.

Regression analysis showed significant positive linear correlations between batch fecundity estimates

(BFE) and TL, gutted body weight (GBW), and age. Total length was the best predictor of batch fecundity (Fig. 5; $BFE = 1.773 \times 10^3(TL) - 1.119 \times 10^6$; r^2=0.600, P<0.0001, n=39); followed by GBW ($BFE = 5.942 \times 10^4(GBW) - 9.517 \times 10^4$; r^2=0.576, P<0.0001, n=35); then age ($BFE = 9.476 \times 10^4(\text{age}) - 1.213 \times 10^5$; r^2=0.474, P<0.0001, n=38).

Spawning frequency: by year, and age × year

Spawning frequency estimates were determined for females >709 mm TL in 1991, >576 mm TL in 1993, and >669 mm TL in 1994. Variations in spawning frequency were significantly different among years tested (t-test, P<0.02). Spawning frequency for females in 1991 was 27 times, with 29.3% (93/317) of individual females spawning at an average of every 3.4 d. Spawning frequency was not determined in 1992 owing to the absence of samples from January and February. Spawning frequency in 1993 was 14 with 16.1% (36/224) of individual females spawning at an average of every 6.2 d. Spawning frequency for 1994 was 8 with 14.0% (18/129) of individual females spawning at an average of every 7.2 d.

Spawning frequency also varied significantly among ages (t-test, P<0.01) and by age × year (ANOVA, P<0.05) for gag (n >5 per age × year) (Table 3; Fig. 6). Age-2 females in 1993 had a spawning frequency = 0, although one spawning female of this age occurred in 1994. Age-3 females in 1991 also had a spawning frequency = 0; 1993 and 1994 spawning frequencies were also low (6 and 7, respectively). Spawning frequency varied the most (6–71) among years for 4- to 8-yr-old gag. Nine year old gag spawned 41 times in 1991. All sample sizes for 10- to 12-yr-old, 16-yr-old, and 26-yr-old gag were inadequate (n<6) for estimation of spawning frequency.

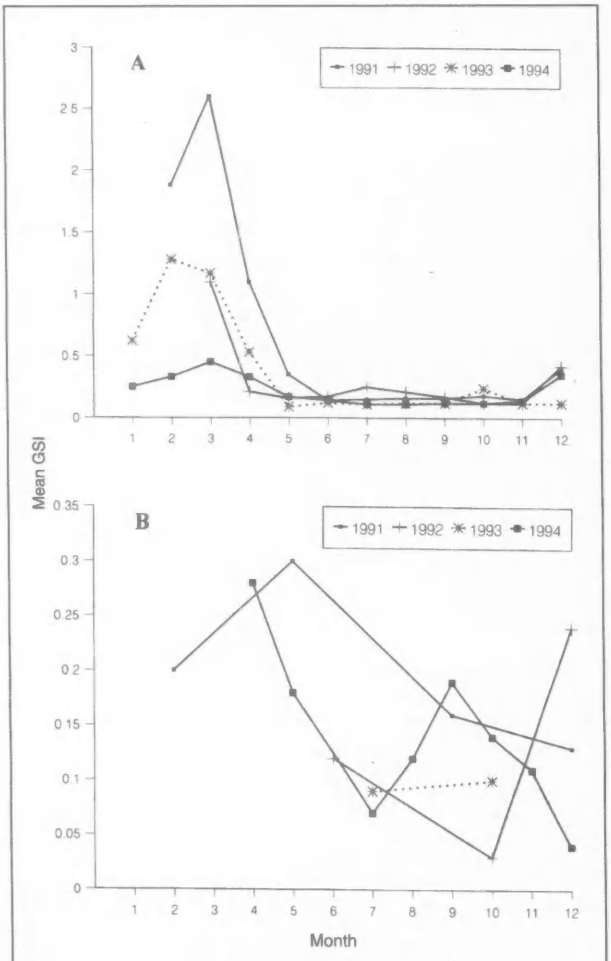

Figure 3

Mean gonadosomatic index (GSI) by month and year for gag. (**A**) females (n=1685) and (**B**) males (n=39) from the northeastern Gulf of Mexico, 1991–94. Note different scales for y axis in A and B.

Annual fecundity

Annual fecundity estimated with spawning frequency estimates by age and year ranged from 0.065 to 61.4 million (Table 4; Fig. 7). Only spawning frequencies for aged fish (n>5 per age and year) were used. Age was an effective predictor of annual fecundity (AFE=9.276 × $10^3(age)^{3.94}$; r^2=0.76, P<0.0001; n=33).

Discussion

We found both the peak and maximum length of the spawning period for gag to be slightly longer than previously determined (e.g. McErlean, 1963; Hood and Schlieder, 1992; Coleman et al., 1996; Koenig et al., 1996) in the Gulf of Mexico. Both GSI and percent frequency of hydrated oocytes and POFs were greatest in February through April, but a few POFs were present in December–January and May–July. Our sampling may not have included peak spawning from 1992 through 1994, as it had in 1991. McErlean (1963), through macroscopic examination of gonads, estimated that spawning occurred January through March. Hood and Schlieder (1992), through histological examination, showed that peak spawning occurred in

February and March and females were spent from December to May. Coleman et al. (1996) and Koenig et al. (1996) used GSIs, fresh "squashes," histological examinations, and juvenile otolith daily increments and found peak spawning to occur in February–March, but some gag were reproductively active from January through mid-May in 1991.

McErlean's (1963) estimates of (annual) fecundity in 7–8 yr-old gag (n=3, 930–946 mm TL) were somewhat similar to our batch fecundity estimates for the same age fish (his and our range of estimates were 0.526–1.457 million and 0.249–0.865 million, respectively) although the exact oocyte size and stage counted by McErlean are unknown. We can infer, however, from the "bright-yellow eggs" he counted (McErlean[3]) that they were vitellogenic (nonhydrated) oocytes because fresh hydrated oocytes are clear. We counted only hydrated oocytes (n=12 fish, 860–1065 mm TL). McErlean's ovary weights averaged 231.1 g, whereas ours averaged 656.7 g. This comparison of ovary weight of similar size and age fish strongly suggests that McErlean's gag were not ready to spawn. Gag population changes between 1961 (McErlean, 1963) and 1991–94 (present study) may also have affected length, age, ovary weight, and fecundity (Johnson et al., 1993).

Our estimates of gag batch fecundity (0.011–0.865 million), spawning frequency by age and year (6–71; see Tables 3 and 4), and annual fecundity (0.065–61.4 million) are similar to those of several multiple spawning, demersal marine species similar to gag in size and longevity. Fitzhugh et al. (1993) estimated mean batch fecundity (1.6 million) and spawning frequency (46, n=25) for black drum, *Pogonias cromis*, whereas Nieland and Wilson (1993) estimated ranges of batch fecundity (0.510–2.42 million), spawning frequency (25–28), and annual fecundity (13.0–67.0 million, n=41) for the same species. Wilson and Nieland (1994) estimated batch fecundity (0.160–3.27 million), and their data indicated a spawning frequency of 1–30 (calculated by the senior author (LAC) of this paper) for red drum, *Sciaenops ocellatus* (n=51). Recently, Collins et al. (1996) estimated batch fecundity (0.001–1.70 million), spawning frequency (21–35), and annual fecundity (0.012–59.7 million) for red snapper, *Lutjanus campechanus* (n=66).

Spawning frequencies and possibly GSIs may be useful in forecasting trends in fishery production. For instance, our estimates of GSI and spawning frequency were greatest during 1991 and 1993, suggesting that population reproductive efforts may have been greater and gag juveniles may have been more

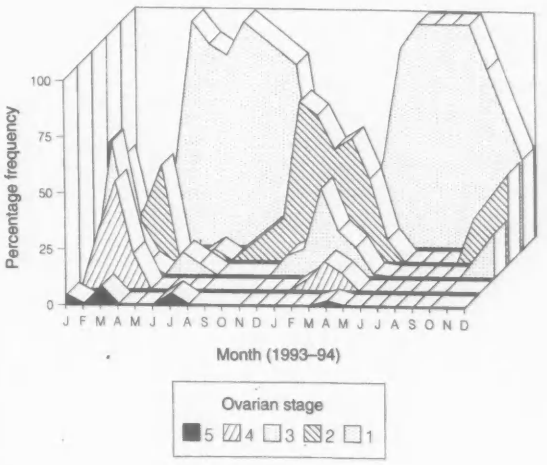

Figure 4

Percentage frequency of gag ovarian stages examined histologically by month and year, 1993–94 (n=636).

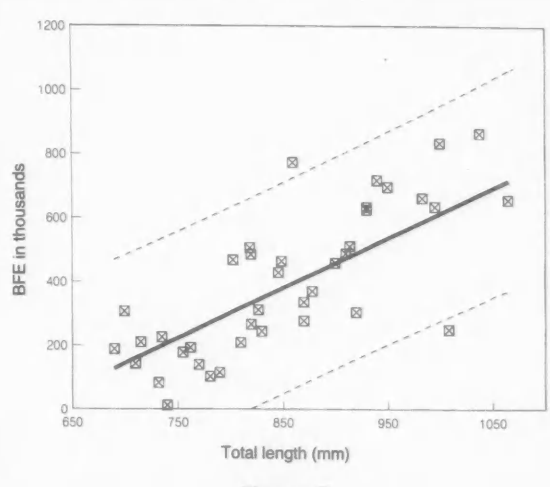

Figure 5

Gag batch fecundity estimates (BFE) plotted and regressed against total length (TL): $BFE = 1.773 \times 10^3 (TL) - 1.119 \times 10^6$ (r^2=0.60, P<0.0001, n=39), and 95% confidence limits (lighter line above and below bold regression line).

[3] McErlean, A. J. [retired]. 1997. 4364 Hickory Shores Blvd., Gulf Breeze, FL 32561. Personal commun.

abundant in these years. This finding is corroborated by studies of Johnson and Koenig (in press), wherein abundance of age-0 gag in north Florida seagrass beds was higher in 1991 and 1993 than it was in 1992 and 1994. Johnson and Koenig (in press) also found that an alternating pattern of abundance was evident in the age structure of the gag fishery from 1984 through 1989, with odd years producing dominant year classes, if the same number of females are assumed to spawn each year.

Table 3

Spawning frequency estimates (SFEs) by age and year for female gag (≥total length (TL) of smallest female with hydrated oocytes (HOs) or postovulatory follicles (POFs) during the spawning season).

Age (yr)	Year	*n*	*n* with HOs/POFs	% with HOs/POFs	SFE
2	91	0	—	—	—
	93	6	0	0	0
	94	1	1	100.0	57
3	91	9	0	0	0
	93	119	8	6.7	6
	94	8	1	12.5	7
4	91	20	6	30.0	28
	93	10	2	20.0	17
	94	78	8	10.3	6
5	91	105	28	26.7	25
	93	34	6	17.6	15
	94	8	1	12.5	7
6	91	8	2	25.0	23
	93	13	4	30.8	26
	94	12	3	25.0	14
7	91	13	1	7.7	7
	93	28	13	46.4	40
	94	2	0	0	0
8	91	6	1	16.7	16
	93	6	5	83.3	71
	94	8	2	25.0	14
9	91	9	4	44.4	41
	93	1	1	100.0	85
	94	2	0	0	0
10–12	91	2	1	50.0	47
	93	0	—	—	—
	94	3	1	33.0	19
16	91	1	0	0	0
	93	0	—	—	—
	94	0	—	—	—
26	91	1	0	0	0
	93	0	—	—	—
	94	0	—	—	—
3–26	91	174	43	24.7	23
2–9	93	217	39	18.0	15
2–12	94	122	17	13.9	8

The scarcity of nondegenerating POFs and the relatively low r^2 values of regression equations suggest that some of our annual fecundity estimates are low, a problem prevalent in some past studies on other species (Nieland and Wilson, 1993; Taylor and Murphy, 1992). The age of POFs is an important factor in judging whether POFs in a sample are from the same spawn as that for hydrated oocytes (Fitzhugh and Hettler, 1995). Delayed preservation in formalin may have caused some incompletely spawned ovaries to appear fully hydrated (if the fragile POFs were lost [Hunter et al., 1985], thus causing low estimates of batch fecundity, spawning fre-

Table 4

Data used for gag annual fecundity estimation, 1991–94. SFE=spawning frequency estimate by age and year.

Catch date	Total length (mm)	Age (yr)	Batch fecundity estimate	SFE	Annual fecundity estimate
1991					
21 Mar	820	5	265,294	25	6,632,350
5 Apr	732	4	82,183	28	2,301,124
5 Apr	755	5	176,552	25	4,413,800
5 Apr	810	5	208,438	25	5,210,950
8 Apr	830	5	243,231	25	6,080,775
8 Apr	870	5	276,416	25	6,910,400
8 Apr	710	5	144,265	25	3,606,625
1993					
25 Feb	870	7	335,275	40	13,411,000
25 Feb	1065	7	657,268	40	26,290,720
25 Feb	1038	8	865,295	71	61,435,945
25 Feb	950	8	696,251	71	49,433,821
20 Mar	860	7	772,158	40	30,886,320
21 Mar	878	8	368,974	71	26,197,154
21 Mar	914	8	510,637	71	36,255,227
22 Mar	983	7	661,993	40	26,479,720
23 Mar	1000	8	834,425	71	59,244,175
23 Mar	930	6	625,159	26	16,254,134
28 Mar	762	3	191,767	6	1,150,602
29 Mar	920	5	302,604	15	4,539,060
29 Mar	715	3	208,878	6	1,253,268
29 Mar	740	3	10,864	6	65,184
29 Mar	820	5	484,514	15	7,267,710
29 Mar	900	5	458,392	15	6,875,880
29 Mar	930	6	633,481	26	16,470,506
29 Mar	995	7	635,329	40	25,413,160
29 Mar	940	7	717,445	40	28,697,800
3 Apr	700	3	304,997	6	1,829,982
3 Apr	735	3	224,684	6	1,348,104
1994					
15 Mar	846	4	428,371	6	2,570,226
15 Mar	690	4	187,216	6	1,123,296
15 Mar	827	5	310,357	7	2,172,499
15 Mar	910	6	487,719	14	6,828,066
6 Apr	1008	8	249,162	14	3,488,268

quency, and annual fecundity). Varying amounts of "missing" hydrated oocytes due to partial spawning would have then caused the low r^2s. An incomplete hydration process in some of the gag is another possible explanation for the low r^2 values; samples were taken from gag caught at different times of the day, causing variable hydration (Hunter et al., 1985). Relatively low r^2 values for the relation between batch fecundity and length and weight were also found for black drum (r^2<0.47, in Nieland and Wilson, 1993) and swordfish, *Ziphias gladius* (r^2<0.41, in Taylor and Murphy, 1992). Because dockside sampling was also used in these studies, delayed preservation may have caused some black drum and swordfish POFs to be missed, thereby causing low r^2 values.

In this study, we used histological sections to identify sex in gag with heavy abdominal pigmentation. Because male behaviors are associated with fish demonstrating this pigment pattern (Gilmore and Jones, 1992), the assumption is widespread that all these fish are males. Yet we found that 5% of such pigmented fish were females. It is possible that these fish were actually in the early stages of sex change, a phase undetectable even with histology.

Our observation of a lining of hydrated oocytes around the outside of the abdominal cavity in gag suggests that the ovary or the oviduct, or both, had ruptured at the time of hydration. This rupture probably did not occur during the fish's capture and handling because the lining of hydrated oocytes was dry and firm when we observed this phenomenon on the boat. A similar rupture may have occurred in a captive population of laboratory-matured female gag where two individuals spontaneously developed hydrated oocytes but did not ovulate; no oocytes were shed although no ovarian rupture was noted, possibly due to the absence of a male.[4] Although the proportion of males required for adequate fertilization is unknown for gag, the sharp decline of males observed by Coleman et al. (1996), Koenig et al. (1996), McGovern et al. (in press), and in this study suggests a restricted availability of males during the spawning period. Ovarian hydration in females in the absence of males could lead to ovarian rupture.

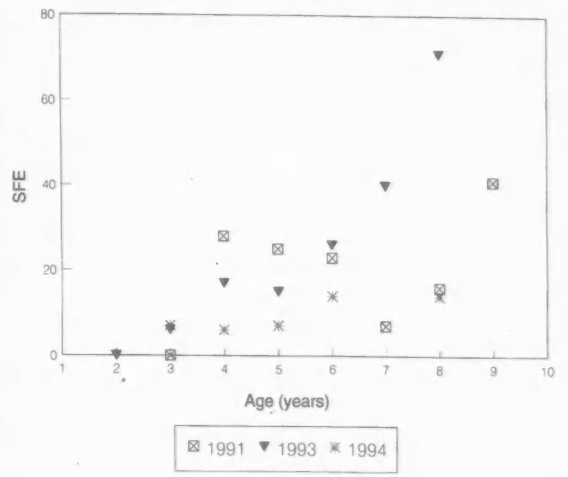

Figure 6

Gag spawning frequency estimates (SFE) by age and year, for ages with n>5 by year.

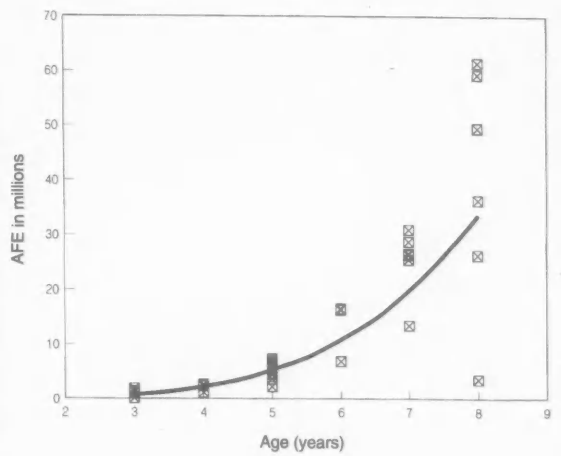

Figure 7

Gag annual fecundity estimates (AFE) plotted and regressed against age in years: $AFE = 9.280 \times 10^3 (age^{3.94})$ (r^2=0.76, P<0.0001, n=33).

Although recent studies have increased our knowledge of gag reproduction, several significant questions remain. Gag appear to spawn at a discrete depth; therefore should only those females from a known spawning area be used for spawning frequency and fecundity estimates? Do fewer males in proportion to females prevent some mature female gag from spawning every year (Coleman et al., 1996;

[4] Carr, W. 1992. Whitney Laboratory, University of Florida, St. Augustine, FL. Personal commun.

Koenig et al., 1996)? Would oocytes hydrate and then be resorbed if there was no male in close proximity? Can gag spawn as females early in the spawning season, change sex, and then spawn as males late in the same season, as suggested for red grouper, *Epinephelus morio*, by Moe (1969)? Would measurement of hormones be a better indicator of the state of transition than our histological examination? Does the possibility that sex change in serranids may occur quickly (captive *Anthias squamipinnis* changed from female to male in two weeks [Fishelson, 1970]) explain why our number of possible early transitional males was low? Questions such as these can only be answered with specifically designed laboratory and field studies.

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We are indebted to many persons and organizations. Several commercial fishermen in the Panama City, Florida, area allowed us to sample their catches, including Captains Ray Ward, Sigurd Smeby, Mark Raffield, Mike Raffield, Dannie Lee, and Steve Smeby. Jerry and Carl Anderson let us routinely sample their seafood markets at Panama City Beach. Charterboat captains Bill Archer and Charles Paprocki also participated in sampling. Special thanks are extended to NMFS Fishery Reporting Specialist Debbie Fable for her help in the field. Bruce Thompson, Jeff Render (deceased), and Cheryl Crowder (Louisiana State University) advised us on methods and ovarian histology. Lewis Bullock, Ron Taylor, and Ruth Reece (Florida Marine Research Institute, St. Petersburg) effectively helped with sampling, methods, and histology. David Wyanski (South Carolina Dep. Natural Resources, Charleston) assisted with identification of transitional males. Reviews by Felicia Coleman, Gary Fitzhugh, Yvonne Sadovy, and Lewis Bullock greatly improved the manuscript. Technical support was provided by Andrew David, John Brusher, Chris Keim, Marc Remy, Sean Murray, Mike Strohmenger, John Dahl, Sandra Neidetcher, Guy Pizzuti, and Sara Heath (NMFS, Panama City). Carol Parker and Betsy Black typed many drafts of this ms. This research was funded by the MARFIN (Marine Fisheries Initiative) Program of the NMFS, Southeast Region (Grant #94 MFIH09).

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Autumn food habits of harbor porpoises, *Phocoena phocoena*, in the Gulf of Maine

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Abstract.—This study describes the stomach contents of 95 harbor porpoises (*Phocoena phocoena*) killed in groundfish gill nets in the Gulf of Maine between September and December, 1989–94. The importance of prey was assessed by frequency of occurrence, numerical proportion, and proportion of ingested mass. Atlantic herring (*Clupea harengus*) was the most important prey, occurring in 78% of noncalf porpoise stomachs and contributing 44% of ingested mass. Pearlsides (*Maurolicus weitzmani*), silver hake (*Merluccius bilinearis*), and red and white hake (*Urophycis* spp.) were common prey items. There were no significant differences among diets of sex and maturity groups, but the calf diet differed significantly from adults in number of Atlantic herring eaten and the total mass of food consumed. At four to seven months of age, calves were eating pearlsides, small silver hake, and euphausiids (*Meganyctiphanes norvegica*) while still nursing.

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Fishery Bulletin 96:428–437 (1998).

Harbor porpoises (*Phocoena phocoena*) from the Bay of Fundy and Gulf of Maine are believed to comprise a single population, hereafter referred to as the Gulf of Maine population (Palka et al., 1996; Wang et al., 1996). To date, studies of the food habits of this population have been restricted to samples collected in the Bay of Fundy during summer, where porpoises feed primarily on Atlantic herring (*Clupea harengus*; Smith and Gaskin, 1974; Recchia and Read, 1989; Smith and Read, 1992). Many porpoises leave the Bay of Fundy in fall, moving southward into the Gulf of Maine (Gaskin, 1977; Gaskin, 1984; Read and Westgate, 1997). During winter, a portion of the population disperses over the continental shelf from New England to North Carolina (Polacheck et al., 1995; Read et al., 1996).

Because of their small size and limited energy stores, harbor porpoises must remain close to food resources to avoid starvation (Koopman, 1994). Moreover, their unusual life history incurs high energetic costs; most females attain sexual maturity at three years of age and give birth to a calf each year (Read and Hohn, 1995). Lactation lasts for at least eight months; thus mature females spend most of their lives simultaneously pregnant and lactating. This intensive reproductive schedule requires calves to become nutritionally independent at a relatively early age, usually before the end of their first year (Smith and Read, 1992).

Large numbers of harbor porpoises are killed each year in gill nets in the Bay of Fundy, Gulf of Maine, and Mid-Atlantic Bight (Read and Gaskin, 1988; Read et al., 1993; Bravington and Bisack, 1996). For the Gulf of Maine, the estimated average annual harbor porpoise bycatch for 1990 to 1995 was 1800 (Bisack[1]). Little is known about the process by which porpoises become entangled in gill nets, and thus efforts are hampered in mitigating this conservation problem. Porpoises may become entangled because they feed on fish species targeted by the fish-

[1] Bisack, K. 1996. Harbor porpoise bycatch estimates in the U.S. Gulf of Maine sink gillnet fishery: 1994 and 1995. Paper presented to the International Whaling Commission Scientific Committee Meeting in Aberdeen, Scotland, June 1996 (in review).

ery or because they feed on the same prey as the target species.

In this paper, we examine the stomach contents of harbor porpoises in the Gulf of Maine during autumn and investigate dietary differences amongst various sex and maturity categories. Our main objectives were to elucidate seasonal changes in the harbor porpoise diet and expand our knowledge of the dynamics between porpoises and their prey that may be responsible for entanglement of porpoises in gill nets.

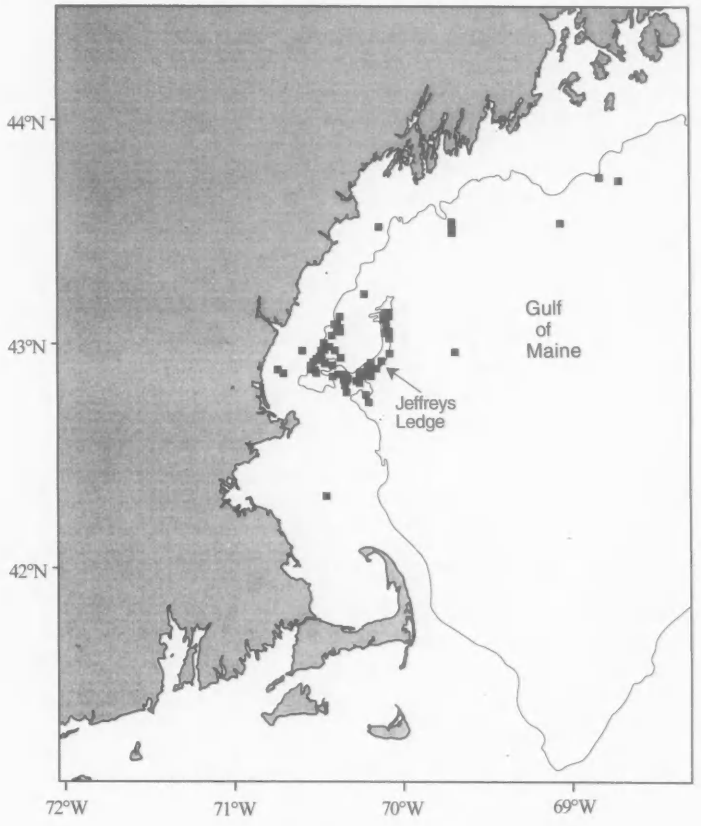

Figure 1

Capture locations of harbor porpoises taken during the autumn (1989–94) in the Gulf of Maine sink gillnet fishery and used in this analysis of food habits. The isobath shown is 91.4 m (50 fathoms).

Methods

Sample collection

The sample consisted of 95 porpoises killed in gill nets during autumn (1 September– 31 December) of 1989 and 1991–94. All porpoises were captured in bottom tending gill nets set for groundfish, principally cod (*Gadus morhua*), pollock (*Pollachius virens*), goosefish (*Lophius americanus*), and several species of flatfish. Most porpoises were taken in the vicinity of Jeffreys Ledge in the west central Gulf of Maine, at water depths between 35 and 185 m (Fig. 1). All samples were obtained by fisheries observers working onboard gillnet vessels. Observers were instructed to retain whole porpoise carcasses whenever possible, but when sea conditions or other factors prevented retention of carcasses, observers excised stomachs in the field. Carcasses and excised stomachs were frozen after the vessels returned to shore (usually 12–48 hours post mortem) for later examination.

On the basis of age (determined from dentinal growth layers and body length; see Read and Hohn, 1995) and reproductive condition (determined by examination of gonads and mammary glands; see Read and Hohn, 1995), porpoises were classified to the following sex, maturity, and reproductive categories: porpoises were considered calves (less than one year of age, not fully weaned), juveniles (older than one year but sexually immature), or sexually mature. The sex and maturity composition of the sample was as follows: (males and females combined) calves = 13; female juveniles = 12; male juveniles = 18; female mature adults = 10; male mature adults = 34; and unknown sex or maturity = 8. Because sample sizes were small, pregnant (n=4), simultaneously pregnant and lactating (n=5), and resting adult females (n=1) were pooled in the "mature female" group for statistical analyses. However, to facilitate comparisons with the findings of Recchia and Read (1989), data for lactating and nonlactating mature females are also presented separately.

Prey identification

The contents of all three stomach chambers were examined in the laboratory. Intact prey were removed first, then loose flesh was decanted. The remaining stomach contents were poured through a 1-mm metal sieve to separate hard parts from liquefied digesta. Solid prey remains used for identification were separated from other skeletal remains by hand. Structures used to identify partially digested food items included sagittal otoliths, dentary bones, and skulls

of teleosts; lower mandibles ("beaks") from cephalopods; tooth cusp plates ("combs") from agnathans; and exoskeletons and eyes from crustaceans. Prey items were identified with the aid of a laboratory reference collection and published guides, including those of Bigelow and Schroeder (1953), Clarke (1986), Harkonen (1986), and Scott and Scott (1988).

Prey importance

Relative food importance in the autumn diet of the harbor porpoise was determined by 1) frequency of occurrence, 2) proportion of numerical abundance, and 3) proportion of total ingested mass. Frequency of occurrence is the percentage of porpoise stomachs containing a particular food type. Proportion of numerical abundance is the number of individuals of a prey species recovered from all stomachs, divided by the total number of all prey from all stomachs. The number of individuals from each fish species in each stomach was determined by summing the number of intact fish and half the number of free otoliths. The number of either upper or lower beaks (whichever were more abundant) from each species was used to determine the number of squid present.

Proportion of prey mass is the percentage of total prey mass in the stomach at the time of death that was represented by a particular species. Reconstituted mass, or the mass of prey prior to ingestion, rather than the existing mass of partially digested prey, was used in this calculation. Reconstituted prey masses were estimated from body lengths of intact prey and the lengths of otoliths or cephalopod beaks (Table 1). If a stomach contained more than 25 otoliths from the same species, all otoliths from that species were counted, and a subsample of 25 was randomly selected and measured. Otoliths were scored on a scale from 0 (undamaged otoliths re-

Table 1

Equations used to estimate length and mass of harbor porpoise prey. ML = mantle length; H = hood length; M = mass; FL = fork length; OL = otolith length; LRL = lower rostral length; and SL = standard length. Length is in millimeters and mass is in grams.

Prey species	Equations	Source
Bathypolypus arcticus (North Atlantic octopus)	$ML = 15.4 + 12.28\,H$ $\ln M = 1.06 + 2.55 \ln H$	Clarke, 1986 Clarke, 1986
Clupea harengus (Atlantic herring)	$FL = 69.23\,OL - 27.48$ $\log M = 3.12 \log FL - 5.41$	Recchia and Read, 1989 Recchia and Read, 1989
Gadus morhua (Atlantic cod)	$\ln(FL/10) = 3.3138 + 1.6235 \ln(OL/10)$ $M = 0.0124\,(FL/10)^{2.93}$	Hunt, 1992 Bowen and Harrison, 1994
Illex illecebrosus (Northern short-fin squid)	$\ln M = 1.773 + 2.4 \ln LRL$	Clarke, 1962
Loligo pealei (Long-fin inshore squid)	$\log ML = 1.767 + 1.4 \log LRL$ $M = 0.25662\,(ML/10)^{2.1582}$	Gannon et al., 1997b Lange and Johnson, 1981
Maurolicus weitzmani[1] (Weitzman's pearlsides)	$FL = 9.82 + 28.75\,OL$ $M = 0.3737\,OL^{2.503}$	Harkonen, 1986 Harkonen, 1986
Merluccius bilinearis (Silver hake)	$FL = 20.9\,L - 0.41$ $\log M = -2.26 + 3.08 \log(FL/10)$	Recchia and Read,1989 Kohler et al., 1970
Peprilus triacanthus[2] (Butterfish)	$SL = -9.15919 + 25.01871\,OL$ $\log M = -0.67576 + 3.222 \log OL$	Present study (r^2=0.983) Present study (r^2=0.924)
Pollachius virens (Pollock)	$\ln(FL/10) = 3.251 + 1.6251 \ln(OL/10)$ $M = 0.0134\,(FL/10)^{2.94}$	Harkonen, 1986 Bowen and Harrison, 1994
Scomber scombrus (Atlantic mackerel)	$FL/10 = 7.33\,OL + 0.37$ $M = 0.00756\,(FL/10)^{3.082}$	Recchia and Read, 1989 Kulka and Stobo, 1981
Sebastes spp.[3] (Rockfish)	$FL = 16.165\,L^{1.224}$ $M = 0.0741\,OL^{3.295}$	Harkonen, 1986 Harkonen, 1986
Urophycis spp.[4] (Red and white hake)	$FL/10 = 1.525\,OL^{1.1456}$ $M = 0.003998\,(FL/10)^{3.1718}$	Clay and Clay, 1991 Clay and Clay, 1991

[1] Taxonomy of the genus *Maurolicus* has been revised recently (Parin and Kobylansky, 1996). The equations used to estimate *M. weitzmani* size are those given by Harkonen (1986) for *M. muelleri*.
[2] Standard length range: 49–153 mm; weight range: 3–104 g; $n = 44$.
[3] Equations given by Harkonen (1986) for *S. marinus*.
[4] Equations given by Clay and Clay (1991) for *U. tenuis*.

trieved from skulls) to 5 (severely degraded, free otoliths) following the methods of Recchia and Read (1989). Otoliths categorized as 3 or higher were not used in size estimations, unless no undamaged otoliths were present. When only damaged otoliths from a particular prey species were present in a porpoise stomach, the available skeletal structures were measured; consequently the reconstituted prey mass for that stomach may have been underestimated (see Jobling and Breiby, 1986; Sekiguchi and Best, 1997)

These three measures of prey importance were applied to data from the 82 noncalf porpoises as a group and to each sex and maturity class. Food habit studies in which different methods are used can yield widely disparate results, making it difficult to draw comparisons between studies (Gannon et al., 1997a, 1997b). Because one of the primary objectives of this research was to obtain information on seasonal changes in the diet, it was important for these data to be treated in a manner similar to those of Recchia and Read (1989) and Smith and Read (1992).

Results

Overall sample

Table 2 lists the numbers and mean sizes of 15 prey taxa recovered from the 95 porpoise stomachs. Atlantic herring (78%), silver hake (*Merluccius bilinearis*, 68%), pearlsides (*Maurolicus weitzmani*, 38%), and red and white hake (*Urophycis* spp., 29%) occurred most frequently in the stomachs of the 74 noncalf porpoises (Table 3). Atlantic herring represented only 7% of the food by proportion of numerical abundance but accounted for 44% of ingested mass. Pearlsides accounted for 67% of food by proportion of numerical abundance but only 3% by ingested mass, owing to their small size. The unknown fish present in porpoise stomachs may have been alewives (*Alosa pseudoharengus*) but this could not be determined with certainty. Both red and white hake (*Urophycis chuss* and *U. tenuis*) were present; however it is difficult to differentiate between small, eroded otoliths from red and white hake, therefore all *Urophycis* otoliths were grouped together. Atlantic hagfish (*Myxine glutinosa*) and euphausiids (*Meganyctiphanes norvegica*) were included in analyses of frequency of occurrence only because the numerical abundance and mass of these two species were difficult to estimate. To allow comparisons to be drawn with the summer diet, data from Recchia and Read (1989) are also given in Table 3.

Figure 2 shows length-frequency distributions for the three most abundant prey: pearlsides, silver hake, and Atlantic herring. On average, Atlantic herring was the largest prey consumed by length (254 mm ±36 SD) with a range from 159 to 339 mm. The average fork length

Table 2

Number and mean sizes of food items present in the stomachs of harbor porpoises sampled in the Gulf of Maine during autumn. ML = mantle length, FL = fork length, and SL = standard length. Present = present in porpoise stomach contents but numerical abundance not determined.

Food item	*n*	Length measurement	Mean length ± SD (mm)	Mean mass ± SD (g)
Bathypolypus arcticus	1	ML	52	48
Clupea harengus	507	FL	254 ± 36	133 ± 56
Gadus morhua	5	FL	241 ± 133	137 ± 201
Illex illecebrosus	18	ML	—	55 ± 22
Loligo pealei	8	ML	129 ± 30	68 ± 29
Maurolicus weitzmani	5898	FL	50 ± 4	0.9 ± 0.2
Meganyctiphanes norvegica	present	—	—	—
Merluccius bilinearis	1605	FL	164 ± 96	65 ± 88
Myxine glutinosa	present	—	—	—
Peprilus triacanthus	38	SL	97 ± 12	24 ± 7
Pollachius virens	76	FL	195 ± 101	136 ± 130
Scomber scombrus	15	FL	224 ± 53	127 ± 91
Sebastes spp.	47	FL	37 ± 3	0.7 ± 0.2
Urophycis spp.	474	FL	159 ± 146	111 ± 172
Unknown fish	4	—	—	—
Milk	present	—	—	—

Table 3

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the diet of noncalf harbor porpoises during autumn in the Gulf of Maine (present study) and summer in the Bay of Fundy (Recchia and Read, 1989).

	Gulf of Maine			Bay of Fundy		
Prey	%FO	%Num	%Mass	%FO	%Num	%Mass
Alosa pseudoharengus	0	0	0	3	<1	—
Bathypolypus arcticus	1	<1	<1	3	<1	<1
Clupea harengus	78	7	44	88	44	64
Gadus morhua	4	<1	<1	14	14	14
Illex illecebrosus	10	<1	<1	6	1	<1
Loligo pealei	4	<1	<1	1	<1	<1
Macrozoarces americanus	0	0	0	2	<1	—
Maurolicus weitzmani	38	67	3	0	0	0
Meganyctiphanes norvegica	12	—	—	—	—	—
Merluccius bilinearis	68	16	22	41	33	19
Myxine glutinosa	7	—	—	—	—	—
Peprilus triacanthus	12	1	1	0	0	0
Pollachius virens	7	1	2	0	0	0
Pleuronectes americanus	0	0	0	<1	<1	—
Scomber scombrus	9	<1	1	6	1	2
Sebastes spp.	11	<1	<1	0	0	0
Urophycis spp.	29	7	26	13	3	2
Unknown fish	1	<1	<1	26	4	—

for silver hake was 163 mm (±95 SD), with the length-frequency distribution showing a strong peak between 30 and 55 mm and another peak between 180 and 205 mm. The mean length of pearlsides was 50 mm (±4 SD), ranging from 40 to 62 mm.

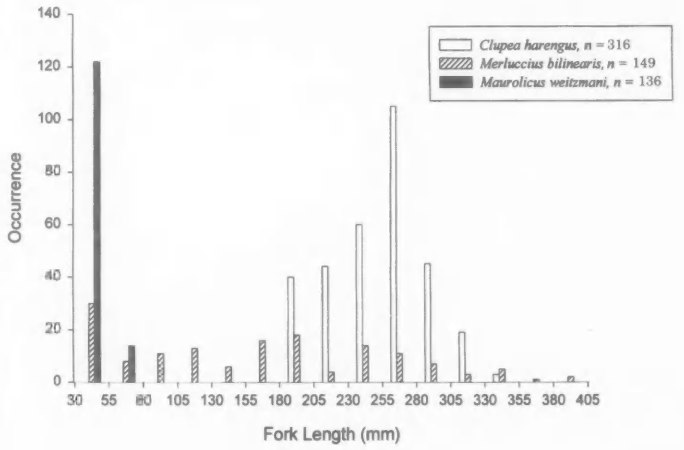

Figure 2

Length-frequency distributions of *Clupea harengus* (Atlantic herring), *Merluccius bilinearis* (silver hake), and *Maurolicus weitzmani* (pearlsides) eaten by harbor porpoises during autumn (1989–94) in the Gulf of Maine.

Diet of sex and maturity categories

The stomach contents of calves differed substantially from those of nutritionally independent porpoises. Pearlsides, silver hake, and euphausiids each occurred in more than half (7/13) of the calf stomachs (Table 4). Pearlsides (72%) and silver hake (26%) were the most numerous prey in calf stomachs and accounted for 53% and 27% of the calf diet by proportion of total mass, respectively. Only 11% of the ingested mass in calf stomachs comprised Atlantic herring (<1% of numerical abundance). Although euphausiids and milk were common in the calf diet, they were excluded from the analyses of

Table 4

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the autumn harbor porpoise diet. Numbers in parentheses refer to frequency of occurrence values found by Smith and Read (1992) for the summer calf diet of the same population in the Bay of Fundy portion of their range.

	Calves (n=13)			Juvenile males (n=18)			Juvenile females (n=12)			Mature males (n=34)			Mature females (n=10)		
Food items	%FO	%Num	%Mass	%FO	%Num	%Mass	%FO	%Num	%Mass	%FO	%Num	%Mass	%FO	%Num	%Mass
Bathypolypus arcticus	0 (0)	0	0	0	0	0	0	0	0	3	<1	<1	0	0	0
Clupea harengus	15 (4)	<1	11	89	8	44	75	38	66	79	6	66	70	20	35
Gadus morhua	0 (0)	0	0	0	0	0	0	0	0	6	<1	1	10	1	1
Illex illecebrosus	0 (0)	0	0	0	0	0	17	1	<1	3	<1	<1	20	1	<1
Loligo pealei	0 (0)	0	0	11	<1	1	0	0	0	3	<1	1	0	0	0
Maurolicus weitzmani	54 (0)	72	53	39	42	1	17	3	<1	41	87	7	30	7	<1
Meganyctiphanes norvegica	54 (63)	—	—	22	—	—	17	—	—	9	—	—	0	—	—
Merluccius bilinearis	54 (0)	26	27	78	38	31	67	50	32	62	4	19	70	65	37
Myxine glutinosa	8 (0)	—	—	0	0	0	8	—	—	3	—	—	40	—	—
Pandalus montagui	0(4)	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Peprilus triacanthus	15 (0)	<1	2	11	1	1	8	1	<1	21	1	1	0	0	0
Pollachius virens	0 (0)	0	0	6	<1	1	0	0	0	9	1	2	20	4	10
Scomber scombrus	0 (0)	0	0	6	<1	1	8	1	<1	15	<1	2	0	0	0
Sebastes spp.	23 (0)	1	<1	17	3	<1	25	1	<1	6	<1	<1	0	0	0
Urophycis spp.	15 (0)	1	7	39	7	21	33	6	1	24	1	1	20	2	18
Unknown fish	0(8)	0	0	0	0	0	0	0	0	0	0	0	10	2	—
Milk	23 (29)	—	—	0	0	0	0	0	0	0	0	0	0	0	0

numerical and mass proportions because it was not possible to quantify their contributions. To facilitate comparisons between seasons, Table 4 also contains data from Smith and Read (1992) on the summer diet of calves from the Bay of Fundy.

Significant differences in stomach contents existed among the five sex and maturity groups regarding the mass proportion of Atlantic herring (no. of cases=87, df=4, K [the Kruskal-Wallis test statistic] =16.077, P=0.003), the number of Atlantic herring present (Table 5; K=18.313, P=0.001), and the existing mass of all stomach contents (K=11.594, P=0.021). The stomach contents of calves were the most divergent of these three categories and when the Kruskal-Wallis tests were repeated with calves excluded, none of the results were significant (Atlantic herring mass proportion: no. of cases=74, df=3, K= 4.284, P=0.232; number of herring: K=1.739, P=0.628; existing mass of stomach contents: K=0.270, P=0.855). No other significant dietary differences were noted between any of the sex and maturity groups at the $\alpha = 0.05$ level.

Qualitative comparisons between lactating and nonlactating mature females revealed that the former had higher frequencies of occurrence for most prey (Table 6). The proportion of total reconstituted mass represented by herring was much higher in nonlactating females. The mass proportions of silver hake and red and white hake were higher in lactating females. It is also interesting to note that three of five lactating females ate hagfish, a frequency far greater than that of any other sex and maturity group.

Discussion

Atlantic herring was the most important prey of harbor porpoises in the Gulf of Maine during autumn; silver hake, red and white hake, and pearlsides were of secondary importance. Although herring was the most significant prey for porpoises in autumn, it was not as dominant as in the summer diet in the Bay of Fundy (Recchia and Read, 1989). Recchia and Read (1989) found Atlantic herring in 88% of noncalf porpoise stomachs, contributing 64% of ingested prey mass; we found herring in 78% of stomachs from noncalves, contributing 44% of prey mass. The relative importance of silver hake, of red and white hake, and of pearlsides was greater in the autumn than in the summer. For example, pearlsides occurred in 38%

Table 5

Prey consumption by harbor porpoises of different maturity and reproductive conditions caught incidentally in Gulf of Maine sink gill nets during autumn 1989–94 (mean ± standard deviation). *Clup.* = *Clupea harengus*, *Maur.* = *Maurolicus weitzmani*, *Mer.* = *Merluccius bilinearis*, and *Uroph.* = *Urophycis* spp.

Porpoise groups	Average mass of individual prey				Average no. of individual prey				Average mass of stomach contents		Average no. of prey taxa
	Clup.	*Maur.*	*Mer.*	*Uroph.*	*Clup.*	*Maur.*	*Mer.*	*Uroph.*	Existing	Reconstituted	
Calves	57 ±40	0.92 ±0.16	19 ±30	42 ±59	0.3 ±0.9	106.5 ±269.6	38.2 ±74.2	1.5 ±5.0	33 ±23	209 ±327	2.4 ±1.4
Juvenile males	131 ±35	0.95 ±0.20	51 ±56	108 ±105	4.2 ±5.0	21.3 ±46.8	19.1 ±38.7	3.6 ±10.8	284 ±288	1304 ±1036	3.2 ±1.3
Juvenile females	140 ±37	0.95 ±0.01	82 ±78	23 ±41	6.9 ±7.5	0.6 ±1.7	9.0 ±19.5	1.0 ±1.8	363 ±356	1389 ±1166	2.8 ±2.4
Mature males	125 ±30	0.95 ±0.05	73 ±103	50 ±46	8.1 ±10.6	117.0 ±372.3	5.6 ±9.5	0.6 ±1.6	274 ±285	1506 ±1526	2.9 ±1.5
Mature females	107 ±28	0.87 ±0.13	77 ±65	339 ±360	4.4 ±7.6	1.6 ±3.2	14.3 ±35.0	0.5 ±1.3	343 ±371	1378 ±1996	2.8 ±1.4

of porpoise stomachs in the autumn, representing 67% of numerical abundance and 3% of food mass but were absent from the summer diet. Recchia and Read (1989) found 11 prey taxa in the stomachs of 127 noncalf porpoises; we found 15 taxa in 82 noncalf stomachs. These results suggest that the diet of this population becomes more diverse as porpoises move out of the Bay of Fundy and into the Gulf of Maine. At the present time, we do not know whether these changes reflect seasonal differences in prey availability, interannual variability in prey populations, or choice on the part of foraging porpoises. Nevertheless, Atlantic herring remains the single most important prey of harbor porpoises in the Gulf of Maine during the autumn.

The size range of prey in the noncalf porpoise diet is larger in fall than in summer (Recchia and Read, 1989). Porpoises continue to eat large prey during autumn, such as adult herring and silver hake, but also eat a substantial number of smaller herring, silver hake, pearlsides, and red and white hake. The large standard deviations in Tables 2 and 5 reflect the wide range of prey sizes eaten.

With the exception of calves, the diet of porpoises did not vary significantly with age or sex. None of the comparisons of forestomach content mass, individual prey mass, or numbers of prey among the four noncalf categories yielded significant differences. Although previous studies of other marine mammal species have found measurable dietary differences between lactating and nonlactating adult females (Bernard and Hohn, 1989; Cockcroft and Ross, 1990; Cheal and Gales, 1991; Kastelein et al., 1993; Young and Cockcroft, 1994; Hobson et al., 1997; Robertson and Chivers, 1997), small sample sizes in this study prevented detailed investigation of potential dietary changes associated with changes in female reproductive condition. Therefore, the findings on diets of lactating and nonlactating mature females should be viewed with caution.

Table 6

Relative food importance, measured by frequency of occurrence (%FO), numerical proportion (%Num), and proportion of total mass (%Mass), in the autumn diets of lactating and nonlactating mature female harbor porpoises.

Prey	Lactating (n=5)			Nonlactating (n=5)		
	% FO	% Num	% Mass	% FO	% Num	% Mass
Clupea harengus	80	7	14	60	52	71
Gadus morhua	20	1	1	0	0	0
Illex illecebrosus	40	1	<1	0	0	0
Maurolicus weitzmani	0	0	0	60	25	<1
Merluccius bilinearis	80	87	52	60	13	10
Myxine glutinosa	60	—	—	20	—	—
Pollachius virens	20	1	5	20	11	19
Urophycis spp.	40	3	28	0	0	0

At four to seven months of age (Read and Hohn, 1995), calves eat a variety of solid foods and continue to supplement their diet by nursing. The large standard deviations for calves in Table 5 may be an indi-

cation that some porpoise calves begin weaning sooner than others. The species composition found in the stomachs of calves in autumn begins to resemble that of older animals. However, the proportions of prey types and sizes of prey differ from those of adults. In autumn, calves eat a greater proportion of pearlsides and euphausiids than do older animals, and the sizes of Atlantic herring and silver hake are smaller than those eaten by older porpoises. Pearlsides, euphausiids, juvenile silver hake, juvenile herring, and juvenile red and white hake appear to be important in the "transitional diet" of calves, as they learn to forage independently. Calves eat a larger quantity and greater diversity of solid food in autumn than in the summer (Smith and Read, 1992). Our observations support and extend the findings of Smith and Read (1992), who suggested that porpoise calves eat euphausiids while their mothers are feeding on other euphausiid predators.

Although harbor porpoises prey on some of the groundfish species targeted by the sink gillnet fishery in the Gulf of Maine, these species contribute just a small fraction of the overall diet. Furthermore, the size range of groundfish consumed by porpoises is much smaller than that targeted by the gillnet fishery because porpoises feed on only the juvenile age classes of those commercial species. The prey that represent the bulk of the porpoise diet (i.e. Atlantic herring, silver hake, and pearlsides) are important forage items for groundfish targeted by the sink gillnet fishery (Langton, 1982). These dietary similarities may lead to overlap between the distributions of groundfish and porpoises, leading both to be caught in the same nets. Silver hake found in porpoise stomachs were highly digested (only 0.1% of silver hake were intact), indicating that they had been consumed some time prior to entanglement. In contrast, herring were often found in a relatively undigested state (15.8% were intact), indicating that many porpoises had been feeding on herring at, or just before, the time of entanglement.

Several potential biases should be kept in mind when interpreting these results. First, all the porpoises we examined had been killed in gill nets anchored to the ocean floor. This capture method may have led to a bias towards demersal prey and against pelagic prey. Without comparable samples collected near the surface, it is not possible to fully address this potential bias. The samples of Recchia and Read (1989) and Smith and Read (1992) may be similarly biased because both studies also obtained samples from porpoises killed in sink gill nets. Second, differential digestion and retention of hard parts are unavoidable in studies of marine mammal stomach contents. Consequently, the importance of species that are resistant to digestion, or that accumulate in porpoise stomachs, will be overestimated. Without empirical data on digestion times for each prey species, it is not possible to evaluate this potential bias fully.

A third potential source of bias arises from the difficulty in discriminating between primary prey (consumed by porpoises) and secondary prey (consumed by porpoise prey). For example, it is possible that small organisms, such as pearlsides, euphausiids, and juvenile silver hake, were secondarily introduced into the porpoise stomach contents. Careful examination of species co-occurrences in porpoise stomachs can provide insights into whether these small organisms were actually eaten by the porpoises. Because many porpoise prey are euphausiid predators (Bigelow and Schroeder, 1953; Langton, 1982; Scott and Scott, 1988), it is difficult to evaluate the likelihood of secondary consumption of euphausiids. However, two calves had euphausiid remains but no other solid food in their stomachs, indicating that they had consumed the euphausiids directly. One calf had pearlsides remains and a herring in its stomach; herring are not considered predators of pearlsides (Bigelow and Schroeder, 1953; Scott and Scott, 1988). Five calves had remains of pearlsides together with juvenile red, white, and silver hake less than 57 mm in length, too small to be predators of pearlsides. We interpret the co-occurrence of pearlsides and juvenile gadiforms in stomachs of calves as an indication of their preference for small prey, rather than as the presence of predators and secondary prey in their stomachs. Among older porpoises, one individual had pearlsides with no other food remains; four had pearlsides and herring; one had 13 pearlsides (totaling 16 grams), a 14-gram butterfish, and a herring; and one had 1100 pearlsides (1052 g) and one butterfish (6 g). Therefore, it is apparent that porpoises do indeed prey directly on euphausiids, pearlsides, and juvenile gadiforms.

In conclusion, the seasonal movements of harbor porpoises are accompanied by changes in diet. Seasonal movements of porpoises may, in fact, be driven by their need to maintain proximity to sufficient concentrations of prey. Assuming that there have not been any major shifts in prey availability between the previous study in the Bay of Fundy (Recchia and Read, 1989) and the present study, the diet of harbor porpoises in the Gulf of Maine during autumn appears to be more diverse than that of harbor porpoises in the Bay of Fundy during summer. The winter ecology of this population probably differs also because many porpoises are believed to leave the Gulf of Maine and Bay of Fundy region during this season. Further information on the diet of this popula-

tion in the winter and spring is required before we can fully assess the ecological relations between harbor porpoises and their prey in this system. We also suggest that further investigation of the ecological relations among Atlantic herring, groundfish, and harbor porpoises may provide information that will allow improved understanding of the causes of porpoise entanglement in gill nets and that will perhaps offer some insight into measures that may mitigate this problem.

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A comparison of two underwater census methods for estimating the abundance of the commercially important blacklip abalone, *Haliotis rubra*

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Abstract.—The blacklip abalone, *Haliotis rubra*, fishery is the most commercially important in Victoria, Australia. Two underwater census methods have been used to survey the status of its stocks. Collection rates from timed searches and counts from radial transects were used to estimate abalone abundance at various locations along the Victoria coast. Radial transect surveys provided precise estimates of abalone abundance; these did not vary significantly between research divers under controlled conditions. During stock monitoring, there were no significant differences among nine of twelve research divers' estimates of abalone abundance from 1339 radial transects sampled at 60 sites during 1992–94. Monte Carlo simulations, used to estimate the probability of detecting annual changes in abalone abundance with each method, provided evidence that radial transects have the potential to detect smaller annual changes in abalone abundance than do timed searches. We suggest that radial transects provide a credible alternative to timed searches and are less subject to potential biases that affect the latter.

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Most analyses of fish stocks are based on catch per unit of effort (CPUE) as a measure of abundance. There appears, however, to be consensus among investigators of abalone that fisheries-dependent methods are inadequate for the estimation of the abundance of abalone stocks. Reasons for this are well documented (Breen, 1992; McShane and Smith, 1992; Prince and Guzmán del Próo, 1993) and include difficulties in estimating the true catch (due in no small part to the prevalence of illegal harvesting) and hyperstability in catch rates despite stock reduction (Hilborn and Walters, 1992). The latter stems from the highly efficient searching behavior of abalone divers who, by targeting large aggregations of abalone, may serially deplete substocks (Prince and Guzmán del Próo, 1993).

Victoria, Australia's second largest abalone-producing state, yields a total annual quota of 1440 metric tons (t) of abalone from approximately 121 km^2 of commercially productive reef complexes distributed along approximately 1500 km of coast (McShane et al., 1986). The Victorian abalone fishing grounds are subdivided into central, eastern, and western zones (Fig. 1), each with its own total allowable catch (TAC). Abundance estimation methods used to survey such an extensive distribution of abalone stocks must be simple so that they may be applied under often adverse sea conditions and so that several sites may be sampled per day.

A reliable survey method for the estimation of abalone abundance has yet to be determined although several diving-based methods are currently used to assess the status of stocks in southern Australia and New Zealand. These include timed searches (McShane, 1994), transect surveys, patch-size estimates (McShane, 1996), change-in-ratio (Nash et al., 1994), and Petersen mark-recapture surveys (Hart and Gorfine, 1997) to provide measures of relative abundance. The intention of such surveys is to provide trends in relative abundance necessary for assessment of stock status. These methods have the advantage of being fishery independent.

However, underwater census methods are characterized by variation between research divers. In particular, relative abundance estimates from timed searches must be standardized between research divers to achieve uniformity in the base sampling unit (10 minutes). Standardization of many research

divers, each represented in the data for relatively few years of a long time series, is problematic. Strip transects can be time consuming and may traverse nonabalone habitat, such as sand; however they provide a consistent base sampling unit among research divers. Patch-size estimates have the advantage of providing a measure of the number and size of aggregations of abalone but are disadvantaged by difficulties in selecting appropriate patch-size categories and maintaining consistency in the area searched during surveys. Change-in-ratio (CIR) has the advantage of not being dependent upon a particular base sampling unit, such as time or area. However, CIR requires that there is no change in one of the two animal categories in the ratio, in this instance prerecruits. This means that the time interval between surveys must be sufficiently short that the effects of growth and natural mortality on the relative abundance of prerecruit abalone can be considered negligible. Mark-recapture (M-R) surveys are time consuming, require that many abalone be tagged, require an estimate of tag loss, may incur incidental mortality due to tagging, assume that the tagged abalone will disperse randomly within the untagged population, and can be affected by migration to and from the study site and into and out of cryptic habitat. If these limitations can be overcome, then M-R can be an effective abundance estimation technique that is free from the research diver effects that characterize other methods.

We introduce a new radial transect survey method for estimating the abundance of abalone and furnish the results of a preliminary comparison with timed searches previously used in Victoria. This new method was developed as an alternative to timed searches because 1) standardization of the effects of research divers who conducted surveys prior to 1992 with those involved in surveys from 1992 onwards was not possible and 2) the depths at many of the reefs surveyed were sufficient to warrant limiting the number of ascents made by research divers each day in order to reduce the divers' risk of decompression illness. We present an analysis of investigations into the effect of research divers on abundance estimates and the probability of detecting interannual changes in abundance with both survey methods. In Victoria, trends in interannual abundance for each management zone have been used as part of an adaptive management strategy. Several successive years of decrease in abundance will trigger consideration for decreasing annual quotas and similarly consideration will be give to increasing quotas where trends in abundance appear to be increasing. Whether quotas are changed and by how much will largely depend on the size of the change in abundance. It is anticipated that this approach will lead to the achievement of quotas that will minimize interannual changes in abundance and thereby optimize sustainable yields from the fishery.

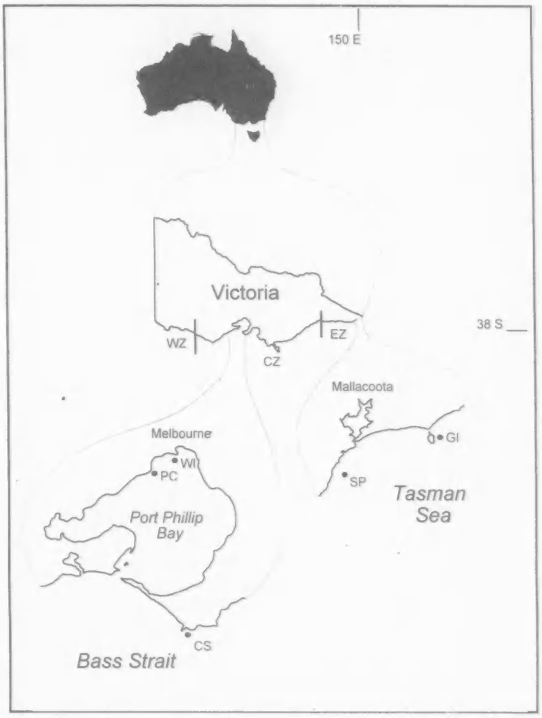

Figure 1

Location of study sites and management zones along the Victorian coast. CS = Cape Schanck; GI = Gabo Island; PC = Point Cook; WI = Williamstown (includes Sticks Reef); SP = Sandpatch Point; CZ = central zone; EZ = eastern zone; WZ = western zone.

Materials and methods

Survey methods

Radial transects Estimates of abalone abundance with radial transects were performed by research divers. At a particular site, a buoyed shot-line (a 20-mm-diameter line anchored by a 20-kg lead weight) was deployed. A stainless steel ring and swivel were used to connect a 35-m long transect-line of 20-mm-diameter line marked at 5-, 15-, and 20-m distances to the lead weight. The transect lines were made from a form of nylon rope that tends to float to the surface, thus decreasing the likelihood of the lines becoming tangled. Dives were made with a surface-sup-

plied breathing apparatus (SSBA) with an umbilical length of 100 m.

Prior to a dive, each diver was randomly allocated three or four compass bearings. On the bottom, each diver oriented himself towards the appropriate compass bearing and tucked the floating transect-line under his arm. Each diver was instructed to use a plastic laboratory tally counter to count, or an abalone iron to collect (depending on the study), emergent abalone larger than 50-mm shell length within an approximately 1-m wide strip from the 5-m mark laterally along the transect line. Abalone smaller than 50 mm were ignored because previous experience had shown that these juveniles were difficult to locate and were likely to be subject to large sampling errors among divers. Where estimates of the abundance of juvenile abalone were required, cryptic habitat within the transect was searched thoroughly by overturning boulders and examining crevices. These searches for juveniles were relatively time consuming. The width of the transect was constrained by the distance from the transect line under the diver's armpit to the hand of the outstretched arm on the opposite side of the diver's body. When abalone were not collected, separate counts of prerecruit abalone, i.e. those individuals smaller than the legal minimum length (LML), and of postrecruited abalone (larger than the LML) were made with a simple measuring gauge for discrimination. Each diver covered a linear distance of 30 m to survey an area of about 30 m^2 per transect. Any part of an aggregation of abalone falling outside the designated 1-m width was not included in the count. Underwater counts were made in instances where the removal of abalone would have interfered with further surveys of the study sites. However, during routine stock monitoring, abalone were collected and taken aboard the research vessel to obtain length-frequency data.

Each diver made additional collections in different directions radiating from the same point before surfacing. Total bottom time for each dive was usually between 30 and 60 minutes.

Timed searches The timed search method was the same as that described by McShane (1994), where each diver made timed searches at randomly selected subsites within each site previously surveyed by radial transects. Commencing at the research vessel's anchor, a pair of divers independently collected as many abalone as possible within a subsite in 10 minutes, using a nylon mesh catch bag and an abalone iron for removing the abalone off rocky substrata. Divers were free to search as much area as their surface air supply hose would allow (about a 100-m radius from the research vessel).

Operator effects on methods

Diver effects on radial transects Variation among divers and each diver's precision with radial transects were investigated at Gabo Island near Mallacoota (Fig. 1). Precision was defined as the level of congruency among an individual diver's repeated counts of the same transect. A team of four scientific divers, each experienced in radial transects, completed two experiments at a fixed site. The objective of the first experiment was to estimate the precision of abalone counts by each diver. This was done by randomly assigning three transects from a set of twelve to each diver and by having them repeat abalone counts along the three allocated transects four times. Precision estimates for each diver were obtained as the quotients of the standard errors of the four counts for each transect divided by their mean count and were compared between divers by a one-way analysis of variance.

The second experiment compared differences among divers' abundance estimates. Each of the four divers completed counts along each of the twelve transects used in the first experiment. An analysis of variance was performed to test the hypothesis that differences among divers' mean abalone counts were not significantly different.

During both experiments, the reference shot-line remained undisturbed. Sea conditions were consistent throughout the day. Surge was slight and horizontal underwater visibility was about 10 m. The study site provided bottom topography that ranged from high relief with deep crevices to open ground with scattered boulders.

Comparison of diver effects on radial transect and timed search survey methods Timed search and radial transect methods were compared during abalone abundance surveys conducted on reefs at Cape Schanck, Point Cook, and Williamstown (Fig. 1). These reefs were selected to provide variety in topography, sea conditions, and abalone population structure. One site was selected at random on each of the three reefs. We tested the hypothesis that there were no significant differences in abalone abundance estimates between research divers for either sampling method. Sea conditions at each site were consistent between sampling methods but varied between the sites. In Port Phillip Bay (Point Cook and Williamstown) wind was slight, swell height was negligible, there was no surge, and horizontal underwater visibility was less than 3 m, whereas at Cape Schanck there was considerable surge (swell height 1–2 m) and underwater visibility was about 6 m.

Two experienced scientific divers, each expert in one of the techniques (>300 dives) but neither hav-

Table 1

Analysis of variance in density estimates, made from radial transect collections, among fifteen sites nested within three locations and among four divers for each of three size classes of *H. rubra* (type IV SS). ns = nonsignificant; * = $P<0.10$; ** = $P<0.05$; *** = $P<0.01$). ω^2 = relative magnitude of variance estimate (%). MS = mean square.

Class	Source	df	MS	F	P	ω^2	Significance
Juvenile	Location	2	0.14	2.42	0.1312	14	ns
	Diver	3	0.05	1.92	0.1593	14	ns
	Location × diver	4	0.04	1.36	0.2822	3	ns
	Site (location)	12	0.06	1.69	0.0904	41	*
	Diver × site (location)	20	0.03	0.75	0.7631	25	ns
	Residual	63	0.04				
Prerecruit	Location	2	2.36	19.24	0.0002	44	***
	Diver	3	0.06	1.10	0.3723	0	ns
	Location × diver	4	0.08	1.32	0.2936	2	ns
	Site (location)	12	0.12	3.56	0.0003	37	***
	Diver × site (location)	21	0.06	1.70	0.0475	18	**
	Residual	81	0.03				
Postrecruit	Location	2	2.60	9.98	0.0028	43	***
	Diver	3	0.33	3.16	0.0461	16	**
	Location × diver	4	0.14	1.30	0.3027	3	ns
	Site (location)	12	0.26	1.95	0.0393	27	*
	Diver × site (location)	21	0.10	0.78	0.7390	11	ns
	Residual	90	0.13				

ing previously used the other method, performed both techniques to census abalone populations at each study site. Abalone counts in four radial transects and four timed collections of 10-min duration were made by each diver at each site so that the effects of divers and methods were fixed and the design balanced. Timed searches were performed after transect counts in each instance to avoid disturbance due to removal of abalone during timed searches.

Separate analyses for each method were made with general linear models to determine the significance of the effects of diver and site on abundance estimates. A combined analysis was not possible because of the different base sampling units for each method. Where Cochran's test indicated significant heterogeneity of variance, data were log-transformed prior to analysis to achieve homoscedasticity (Winer, 1971). Diver × site interaction was omitted from the analyses presented in Table 1 because preliminary analyses showed this effect to be nonsignificant.

Trial stock surveys

The effects of divers on the detection of differences in abundance were further investigated during trial surveys of substocks at Gabo Island and Sandpatch Point near Mallacoota and Sticks Reef near Altona in Port Phillip Bay (Fig. 1). These surveys were aimed at determining how well variation among several locations was detected with this method when it was applied over a spatial scale comparable to that used in routine stock surveys.

Five sampling sites were randomly selected at each location, and for each site, three out of five divers were selected to undertake the sampling depending on their availability and fitness to dive. Two to three sites at each location were sampled during each day of the surveys. At each site, each diver made three replicate radial transect collections of emergent prerecruit and postrecruited abalone. Each diver also collected juvenile abalone (<80 mm) in one of their three assigned transects by searching cryptic habitat and turning over small boulders. All abalone collected were brought on board the research vessel, and the maximum shell length of each was measured to the nearest mm.

Analysis of variance of the mixed linear model was used to test the effects of locations, sites nested within locations, and divers on abundance estimates. The SAS® general linear model (GLM) procedure was used (SAS Institute, Inc., 1989). Separate analyses were performed for three size classes of abalone (juvenile <80 mm, 80-mm ≤ prerecruit < LML, and postrecruit ≥ LML). Data were converted to number per m^2.

The relative treatment magnitude, omega squared (ω^2), for each effect in the GLM was calculated (Keppel, 1991).

Design of stock monitoring program

Abundance estimates of abalone stocks in Victoria were made annually at 60 sites, using radial transects during 1992 to 1994. These estimates were made during routine stock surveys for the Victorian program for abalone stock assessment. At each site, nine replicate abalone collections were made. Sites were selected from abalone habitat with commercial quantities of abalone. During 1992, sites for radial transect surveys were initially chosen at random from between the 5-m and 18-m isobaths to avoid the wave-break zone and to minimize hyperbaric exposure. Accurate navigational fixes were made at each site with a global positioning system (GPS). During successive years each site was resurveyed after having been located with GPS. This mixed sampling design has been shown to have greater power than nested designs for benthic monitoring and avoids the potential bias of fixed designs (Van der Meer, 1997).

Application of methods to stock monitoring

An analysis of variance was applied to results from stock monitoring surveys to determine the interannual variation in abundance for each zone. This was in the form of a mixed linear model in the SAS® general linear model procedure.

The relative treatment magnitude for each effect in the GLM was calculated with the same procedure as that used in the trial stock surveys.

The effect of differences between research divers on abalone abundance estimates from radial transects was further investigated (with two- and three-way interactions omitted) across all zones from an analysis of 1992–94 stock surveys. During each field survey of a group of adjacent sampling sites, the dive team was composed of three or four out of a possible twelve divers. Differences in the composition of dive teams between surveys occurred for logistical reasons. At each site three divers performed three radial transects each where the allocation of directions for these transects among divers was random. Differences among divers were compared by using Ryan's test (Day and Quinn, 1989), and the effect of diver experience on abundance estimates was determined by regressing divers' mean collections of abalone per transect against the number of transects each diver performed.

Power to detect changes in abundance

Monte Carlo simulations were made to estimate the probability of detecting cumulative annual changes in abundance. The simulations were based on data from stock surveys conducted during 1992 and 1993 that employed radial transects as well as data from 1989 and 1991 surveys based on timed searches. Scenarios involving different combinations of annual change increments (increases) and number of years sampled were each simulated 200 times for each management zone (i.e. central, eastern and western; Fig. 1). Divers were randomly selected from those who participated in the surveys, and the abundance estimates for each radial transect were adjusted for the diver factor and variation within each site, whereas the abundance estimates for timed searches were standardized by using a linear regression between pairs of divers (McShane, 1994). The respective analyses of variance used to analyze the stock survey data for each method were applied to each simulation, and the proportion of tests that showed a significant (α=0.05) annual change in abundance (year effect) was calculated. The proportion of significant results for each management zone was then plotted against the number of years simulated for each increment level. A smoothing function was applied to each curve to eliminate fluctuations due to changes in confidence levels among years in the series.

Results

Operator effects on methods

Diver effects on radial transects During the first experiment at Gabo Island, the precision ($SE/\bar{x}$) of the divers' abalone counts for each transect ranged from 0.04 to 0.27. Cochran's test showed the divers' variances of precision to be homoscedastic (α=0.01). Differences among divers' mean precision values were not significantly different (F=1.43; df =3, 8; P>0.10). Collectively, the four groups of twelve estimates of abundance represent four identical surveys of the same site which yielded similar mean abundance estimates on each occasion (Fig. 2). Estimates of mean abalone abundance for the site during the second experiment were also similar (Fig. 3) and no significant differences were detected among the four divers (F=0.01; df=3, 33; P>0.10).

Comparison of diver effects on radial transect and timed search survey methods There were no significant differences between the two divers when using radial transects (F=0.19; df=1, 2; P>0.10) nor were there significant differences when using timed searches (F=7.31; df=1, 2; P>0.10). Notably, the differences between the divers' mean abundance estimates (Fig. 4) were much smaller for radial transects

(effect size=9%) than for timed searches (effect size=44%); thus power in the analysis was likely to be low.

Trial stock surveys with radial transects

There were significant differences in density between all locations for the prerecruit and postrecruit size classes, but locations were not significantly different for juvenile abalone (Table 1). Locations and sites within locations accounted for most of the variation in density of pre- and postrecruit abalone. Significant differences between divers occurred for postrecruits, but the magnitude of the variance effect for divers was only about one third of the variance effect for sites. Sites varied significantly within locations for each size class; for juveniles and post recruits this was at the 10% confidence level, and for prerecruits at the 1% confidence level. Only one interaction effect, diver × site (location) for prerecruit density, was significant.

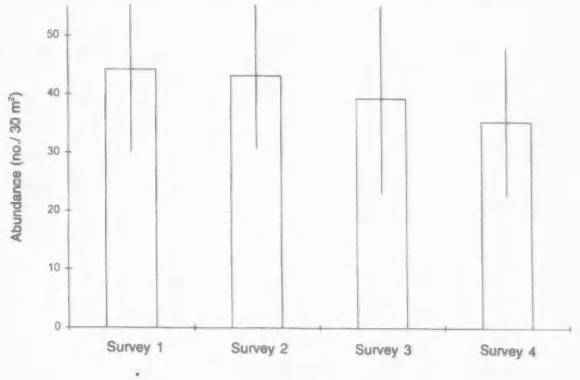

Figure 2

Comparison of mean abundance estimates of *H. rubra* at Gabo Island among surveys using radial transects. Error bars are 95% confidence limits.

Application of methods to stock monitoring

Variation in abalone abundance estimates from both methods showed significant diver effects in two out of three instances (Tables 2 and 3). However, the only significant year effect detected was for estimates from radial transect surveys in the central zone of the fishery. The lack of a significant diver effect in this instance may have increased the power to detect a year effect. Consistent with the high spatial variability that characterizes abalone populations, site effects were significant in all instances. Year × site interactions were significant in two instances for each method, indicating that interannual changes in abundance varied among sites within the affected zones. Only one year × diver interaction was significant and because some divers were not represented in each year, the interpretation of this effect in this instance is problematic.

For each method only a relatively small amount of the variation in abundance could be attributed to the effect of year. Sites generally accounted for most of

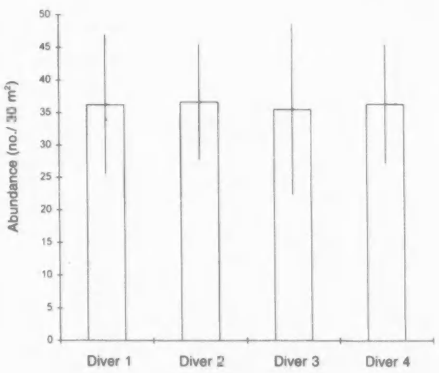

Figure 3

Comparison of mean abundance estimates of *H. rubra* at Gabo Island among divers using radial transects. Error bars are 95% confidence limits.

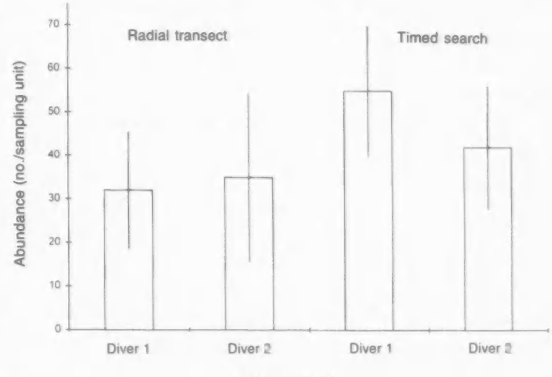

Figure 4

Diver effects on mean abundance estimates of *H. rubra* for each survey method. Error bars are 95% confidence limits; base sampling units were 30 m² for radial transects and 10 min for timed searches.

Table 2

Analysis of variance for interannual differences in abundance estimates of *H. rubra* for each of Victoria's fishery management zones, made from timed collection surveys, during 1989–91 (type IV SS). (ns = nonsignificant; * = $P<0.10$; ** = $P<0.05$; *** = $P<0.01$). ω^2 = relative magnitude of variance estimate (%).

Management zone	Source	df	MS	F	P	ω^2	Significance
Central	Year	2	136.60	0.69	0.5141	1	ns
	Site	28	286.04	2.42	0.0008	45	***
	Diver	16	205.08	1.73	0.0525	13	*
	Diver × site	83	92.85	0.79	0.8714	20	ns
	Year × site	21	198.87	1.68	0.0468	16	*
	Year × diver	4	25.70	0.19	0.9404	4	ns
	Year × site × diver	10	138.32	1.17	0.3207	2	ns
	Residual	98	118.28				
Eastern	Year	2	203.64	1.30	0.2914	1	ns
	Site	13	181.97	1.99	0.0230	18	**
	Diver	8	54.01	0.59	0.7863	5	ns
	Diver × site	71	77.91	0.85	0.7872	15	ns
	Year × site	24	156.81	1.71	0.0241	24	**
	Year × diver	4	60.83	1.59	0.1961	3	ns
	Year × site × diver	41	38.34	0.42	0.9993	34	ns
	Residual	224	91.66				
Western	Year	2	160.84	1.40	0.2814	1	ns
	Site	15	836.77	5.32	0.0001	67	***
	Diver	5	779.21	4.95	0.0008	20	***
	Diver ×(site	43	186.48	1.18	0.2755	8	ns
	Year × site	13	114.87	0.73	0.7262	4	ns
	Year × diver	0	—	—	—	—	—
	Year × site × diver	0	—	—	—	—	—
	Residual	54	157.38				

the variation in the ANOVA model. For timed searches the variance estimate for diver effects was about one third that for sites; however for transects, the relativity between diver and site variance effects was more variable. The values for the relative magnitude of variance estimates attributable to divers were similar between the two methods.

Mean abundance estimates from radial transects during stock monitoring surveys varied significantly among divers; divers 4 and 5 in particular collected relatively fewer abalone per transect and diver 8 collecting more than the other divers (Table 4). Ryan's test did not reveal a significant difference between the remaining nine divers' mean relative abundance estimates (Table 4). A regression of the divers' mean relative abundance estimates against the respective numbers of radial transects performed (r^2=0.01, n= 1339) showed that the slope of the relationship was not significantly different from zero (P>0.10).

Power to detect changes in abundance

The number of years of sampling required for an 80% or greater predicted probability of detecting a significant cumulative change in abundance with radial transects ranged from 1–3 years for all zones. The western zone required 3 years for 2.5% and 5% increments to become significant on 80% of occasions and 2 years for the 10% increment. The other two zones required only one year for all increments to become significant (Fig. 5A).

In contrast, timed searches (Fig. 5B) required three years to detect a cumulative annual increase of 10% in the central zone with 80% probability, and five years for the same size change in both the eastern and western zones. In the eastern zone the probability of detecting increases with timed searches was similar to that for the central zone with transects. In this instance only one year was required to have an 80% probability of detecting each increment of change.

Discussion

Radial transects provided precise estimates of abalone abundance and did not vary significantly between different divers in three of the investigations made during this study. However, the importance of selecting scientific divers with aptitude for these types of surveys is underscored by the fact that three

Table 3

Analysis of variance for interannual differences in abundance estimates of *H. rubra* for each of Victoria's fishery management zones, made from radial transect surveys, during 1992–94 (type IV SS). ns = nonsignificant; * = $P<0.10$; ** = $P<0.05$; *** = $P<0.01$. ω^2 = relative magnitude of variance estimate (%).

Management zone	Source	df	MS	F	P	ω^2	Significance
Central	Year	2	515.43	4.08	0.0222	3	**
	Site	29	378.00	5.04	0.0001	54	***
	Diver	10	93.24	1.24	0.2611	1	ns
	Diver × site	123	47.16	0.63	0.9989	21	ns
	Year × site	56	126.36	1.69	0.0022	18	***
	Year × diver	5	31.23	0.49	0.7842	1	ns
	Year × site × diver	35	64.17	0.86	0.7066	2	ns
	Residual	479	75.00				
Eastern	Year	2	130.23	0.87	0.4312	0	ns
	Site	14	801.99	5.33	0.0001	38	***
	Diver	5	1170.54	7.78	0.0001	21	***
	Diver × site	46	274.05	1.82	0.0021	23	***
	Year × site	28	150.21	1.00	0.4728	0	ns
	Year × diver	4	301.05	5.22	0.0057	11	***
	Year × site × diver	18	57.69	0.38	0.9899	7	ns
	Residual	242	150.48				
Western	Year	2	36.54	2.30	0.1214	1	ns
	Site	12	261.00	7.14	0.0001	41	***
	Diver	7	100.08	2.74	0.0096	7	***
	Diver × site	40	47.61	1.30	0.1201	7	ns
	Year × site	24	147.51	4.03	0.0001	40	***
	Year × diver	6	65.70	1.31	0.3016	1	ns
	Year × site × diver	18	50.04	1.37	0.1201	4	ns
	Residual	225	36.54				

divers' mean transect collections differed significantly from the remaining nine divers during three annual abalone stock surveys. During routine monitoring, two divers (4 and 5) consistently collected less abalone than the others and frequently aborted dives after having failed to complete all their allocated transects. Reasons given for terminating their dives included problems with middle ear equalization, difficulty coping with the surge and backwash created by waves, and fouling of lines and air hoses due to entanglement. These observations concur with Shepherd (1985) who found that surge and kelp density were two significant factors affecting research diver efficiency in underwater censuses of abalone populations. In contrast to divers 4 and 5, diver 8 consistently collected more abalone than the other research divers. However, diver 8 participated only in those parts of the study conducted in the eastern zone, where abalone stocks are generally more abundant. Also, as an ex-abalone diver, diver 8 could reasonably be expected to possess a superior ability in performing abalone searches and collections that may have biased his estimates.

These observations suggest that some divers may not possess the aptitude required to conduct underwater censuses and highlight the need for understanding the nature of research being conducted. The ability to work at sea in often arduous conditions, discipline in adherence to sampling protocols, and

Table 4

Mean number (least squares) of *H. rubra* collected per transect by each diver during 1992–94 Victorian abalone stock surveys. Vertical bars in "ns" column indicate groups of means that were not detected as significantly different by Ryan's test (α=0.05). ls = least squares; SE = standard error of the least squares means.

Diver	n	ls mean	± SE	ns
8	36	19.48	1.92	|
9	147	16.03	0.95	|
1	467	12.62	0.53	|
12	38	12.00	1.87	|
3	408	11.26	0.57	|
11	66	10.74	1.42	|
7	6	10.50	4.71	|
6	17	10.03	2.80	|
2	119	10.02	1.06	|
10	15	9.73	2.98	|
4	107	7.83	1.12	|
5	12	3.58	3.33	|

the importance of avoiding a competitive atmosphere in which bagging the most abalone becomes the objective are essential characteristics of an effective abalone survey team. The problem of competition implies that nondestructive sampling, such as counting, may reduce potential bias associated with col-

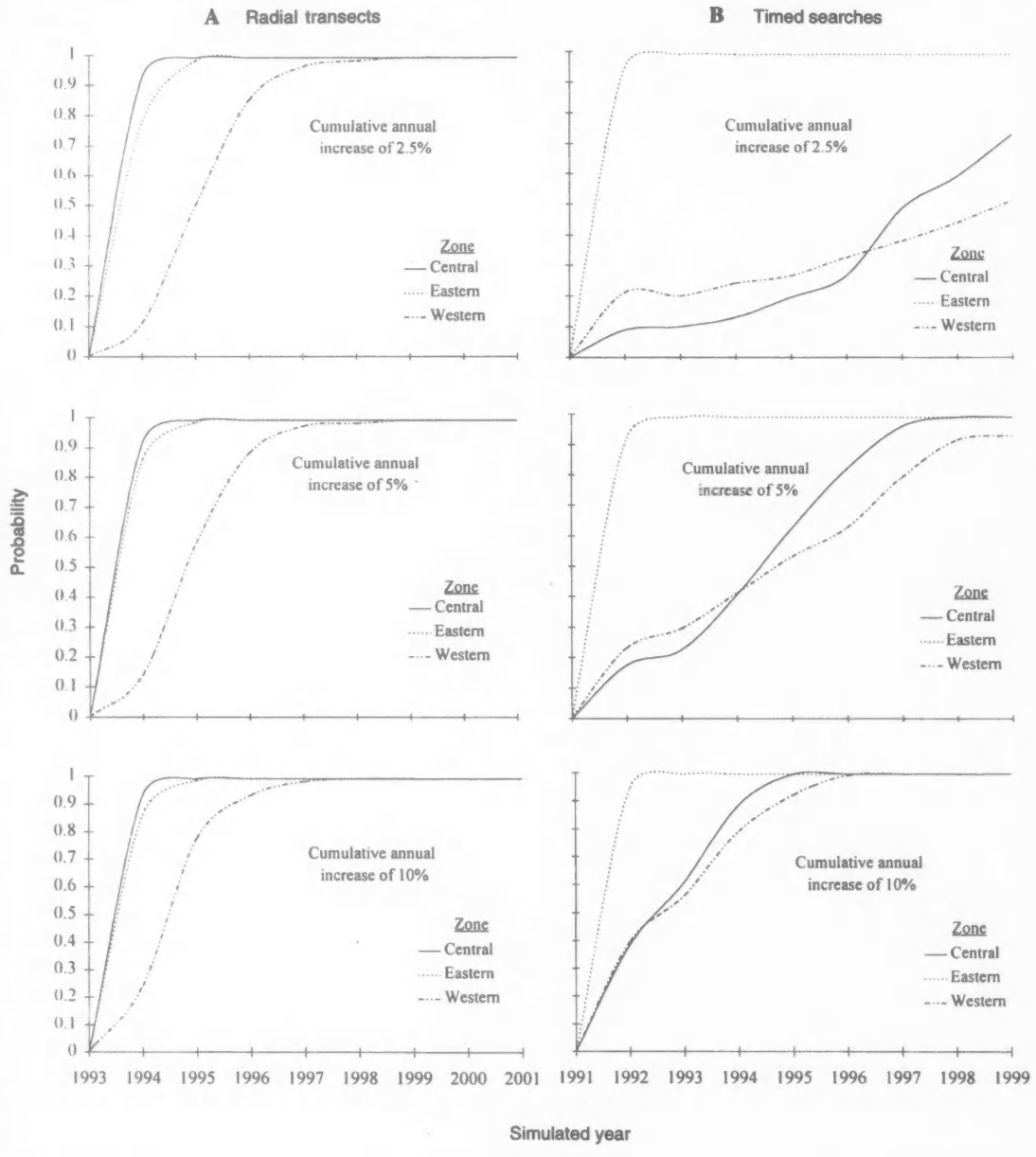

Figure 5

Predicted probabilities for detecting cumulative annual changes in *H. rubra* abundance from (**A**) radial transect surveys and (**B**) timed searches.

lecting. Indeed, the diver who consistently collected more abalone from transects during routine stock surveys was not significantly different from other members of the dive team when only counts of abalone were required. Similarly, McShane (1995) found that by reducing the handling time involved with the collection of large numbers of abalone from dense aggregations he reduced the operator bias in the estimation of patch frequency. Counting also has the advantage of considerably reducing the time needed to complete each transect. However, collecting becomes necessary when length-frequency data are required because in-situ measurements are impractical under the surgy conditions commonly encountered.

Experience in the radial transect method did not have a significant influence on the number of abalone estimated despite the fact that the number of transects completed per diver varyied over a wide range (6–438 transects). Differences among divers are expected when those who sampled at only a few locations are compared with divers who sampled over a larger range of abalone populations. This expectation is supported by the lower standard deviations associated with the mean collections per transect of the less experienced divers.

The standard deviations of the divers' mean relative abundance estimates from radial transects were relatively large, especially for those divers who had completed many such transects. This large range reflects the high spatial variability in abalone densities both within and between sampling sites which is evident from the relatively large proportion of variance contributed by location and site effects. During the trial stock surveys, variation among sites within locations was mostly similar to the variation among locations (except for juveniles). Although higher precision in abundance estimates may be obtained by sampling on a small scale, our results support the notion that abalone distributions are variable over the range of spatial scales commonly used to census abalone populations. Under these circumstances stratification of sites may provide little increase in the power of population surveys to detect interannual changes in abundance. The higher proportion of variance between sites in relation to locations with sampling juvenile abalone was not unexpected because of the smaller number of replicates and the greater degree of difficulty in observing this cryptic size class (Nash et al., 1994). The importance of adopting a sampling design that minimizes spatial effects is highlighted by the low proportion of the total variation attributable to the year effect. The mixed design we used provided a compromise between the advantages offered by fixed designs in reducing within-site variability and those offered by random designs in improving the precision of estimates of site means. The consequent increase in power over a random design has allowed us to economize on the number of sites sampled annually.

The use of transects to estimate the abundance of abalone stocks has been criticized (McShane, 1994) as a time-consuming approach that does not allow for the patchy nature of abalone distributions over relatively small spatial scales. However, strip transects provide an objective and reproducible approach to population surveys that appear to be somewhat less affected by research diver differences than are observations made against time. Our results demonstrate that variability among most scientific divers in the use of both radial transects and timed searches generally has a relatively small effect on variation in abalone abundance estimates. This finding suggests that standardization of abundance data from underwater censuses of abalone populations may be unnecessary. Because adaptive approaches to the setting of TACs require a time series of abundance indices, it is unlikely that all scientific dive team members will be retained for the required period. Thus effects of variation between diver and year will confound abundance estimates and interannual variation in abundance. The general linear model we used to analyze abalone abundance data includes the effect of variation among divers. For both methods, diver effects were smaller than site effects. Previous analyses of timed search estimates involved standardization to eliminate diver effects, with the assumption that all differences between within-site replicates were due to diver variation (McShane and Smith, 1990). With this approach there is a risk of underestimating the variances of mean abalone abundances because variation between divers is confounded with intrasite variation. Another problem with standardization of data to eliminate diver effects prior to analysis is the resulting confidence levels associated with performing multiple regressions between different diver pairs. The greater the number of divers the lower the level of confidence. This finding contrasts with the higher confidence level provided by the general linear models procedure, which takes account of diver × site interaction, thereby requiring only one comparison among divers.

The radial transect method is a credible alternative to timed searches for the conduct of underwater census of abalone. The notion that transect surveys are inefficient and time consuming ignores the importance of how the transects are applied. The number of radial transects that can be completed in a typical day of sampling compares favorably with the number of timed searches that can be completed within the same period. When timed searches were

used to survey Victorian abalone stocks, about 20–28 samples were completed daily; the radial transect method provides 27 samples during a typical day and requires only one-third the number of ascents per diver, reducing the risk of decompression illness (Marks and Fallowfield, 1994; Oxer, 1994). As with timed searches, the radial transect method has been successfully applied under rough sea conditions typical of the exposed coastal reefs colonized by abalone.

McShane and Smith (1990) identified the similarity between the timed search method and the techniques employed by commercial abalone divers to target aggregations of abalone. From this similarity one can reasonably infer that in some instances the abalone collection rate of research divers may exhibit (albeit over a smaller spatial scale) the hyperstability that characterizes the catch per unit of effort of commercial abalone divers. Indeed, in a study involving intensive experimental fishing McShane and Smith (1989) could not detect a significant difference between pre- and postfishing abundance estimates of postrecruited abalone from timed searches despite a 50% decrease in CPUE. In his discussion of a patch-frequency estimation method, McShane (1995) noted the bias in timed searches when a large proportion of the search time is spent collecting abalone from dense aggregations. Radial transects target a specific area (30 m^2); consequently handling time does not affect the numbers of abalone counted or collected and divers are unable to target aggregations to the exclusion of more sparsely distributed abalone. Therefore it is reasonable to expect that surveys based on radial transects more accurately reflect true abalone abundance than do those based on timed searches.

Although there is no doubt that dense patches of abalone are important with respect to fishing and the maintenance of profitable catch rates (McShane, 1995), recent work on *H. rubra* in Victoria (Officer[1]) has demonstrated the importance of postfishing movement and reaggregation in maintaining these patches. The Victorian studies also showed that dense patches contributed most of the variation in abundance estimates and that the standard deviations of samples of sparsely distributed abalone were relatively small. It is from these sparsely distributed abalone, and those occupying cryptic habitat, that reaggregation appears to have occurred. Further research is required to determine the relative importance of sparsely distributed abalone in assessing the impact of fishing. Abundance estimates from transect sampling may prove to be more effective indicators of the size of stocks if dense aggregations are excluded from surveys.

Because the application of radial transects avoids targeting some emergent abalone to the exclusion of others, there is less potential for divers to bias their sample towards larger abalone as may occur with timed searches. By measuring the length of each abalone collected, separate estimates of abundance for prerecruit (shorter than the legal minimum length) and postrecruit (recruited to the stock) abalone can be made. Timed searches do not necessarily permit this separation of prerecruits from postrecruits because of the potential for divers to collect larger, more accessible abalone at the expense of smaller abalone. Timed search estimates of abundance reported in McShane and Smith (1989) show an almost threefold increase in prerecruits after fishing, suggesting that abundances of prerecruits may have been underestimated prior to fishing because of the prevalence of postrecruits.

Our trial stock surveys provided evidence that the transect method has the power to detect differences in abalone abundance (among locations and sites) and is robust in respect to differences in divers' abilities to perform the method. Moreover, annual stock surveys based on radial transects were able to detect a significant change in abundance between consecutive years and had a high power of detecting smaller effect sizes over 2–3 years, thus showing their usefulness as an effective stock monitoring tool. The radial transect method as it is currently applied for monitoring Victorian abalone stocks should have sufficient power to detect changes in abundance of about 10% after 3 years sampling. Monte Carlo simulations showed that surveys based on timed searches generally would require several years of sampling and consequently would have lower power than radial transect surveys in detecting the same rate of change. The simulation results for the eastern zone, where it was predicted that only one year would be required for a 2.5% change, proved to be the only exception. However, unlike the timed search sampling of the central and western zones, all sites in the eastern zone were sampled twice annually during 1989–91. This additional sampling would be expected to increase substantially the statistical power to detect changes in abundance.

Surveys based on radial transects have been used to monitor *H. rubra* stocks in the Victorian abalone fishery since 1992 with the objective of establishing a temporal series of abundance data to assist managers in determining sustainable levels of fishing. In monitoring Victoria's abalone stocks, the aim is to detect an overall change in abundance across a man-

[1] Officer, R. 1997. Marine and Freshwater Resources Institute, PO Box 114, Queenscliff, Victoria 3225, Australia. Unpubl. manuscript.

agement zone against a background of increases and decreases at different sites within that zone. Although the Monte Carlo simulations predict that, with the use of transects, such overall changes should become detectable within several years, it is obvious that a much longer time series than three years is required to determine if significant interannual changes form part of a trend in abundance. In addition to the temporal scale required for effective monitoring of abalone stocks, there is also the issue of selecting an appropriate spatial scale over which to sample. Many abalone fisheries are managed in spatial units involving several hundreds of kilometres of coastline, and the relatively high cost of fishery-independent surveys ensures that compromises must be made to maximize the benefits from stock assessment programs. Consequently, the biologist investigating abalone is faced with selecting between a limited number of intensive surveys of substocks over small spatial scales and extensive surveys that are less detailed but at the scale over which the fishery is managed (McShane et al., 1994). In their discussion of the design of surveys for abundance indices, Hilborn and Walters (1992) favored extensive surveys with low sampling intensities that cover the entire fishing grounds. Their preference for many sampling stations and minimal effort per station has recently been supported by Van der Meer's (1997) study. This is the approach we are currently using to survey abalone stocks in Victoria, although we maintain relatively high within-site replication to allow greater precision for site means. Whether power is traded off against precision depends on the extent to which inferences are to be drawn regarding individual sites.

Acknowledgments

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Age, growth, and mortality of black drum, *Pogonias cromis*, in the Chesapeake Bay region

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Abstract.—We used otolith ageing to describe the population dynamics of black drum, *Pogonias cromis*, collected over a three-year period from the Chesapeake Bay region's commercial and recreational fisheries. Black drum average age, total length, and weight were 26 years, 109.5 cm, and 22.1 kg respectively. The oldest fish was 59 years and fish older than 50 years were present in the catch from 1990 to 1992. Growth in length slowed by age 20, whereas growth in weight did not slow until age 45. A von Bertalanffy growth function was fitted to our data (L_∞= 117.3 cm, K=0.105, t_0=–2.3 yr) and was similar to that for northeast Florida, but dissimilar to that for the Gulf of Mexico. Fish grow slower but reach larger sizes in the Atlantic than in the Gulf. Estimates of instantaneous total mortality, Z, from maximum age and catch-curve analyses were low, 0.08–0.13, indicating that fishing mortality is also low in the Chesapeake Bay region. Studies to date lend support to the hypothesis that black drum from the east coast of the United States are from a common stock. The fishery of the Chesapeake Bay region is made up of old, large migrants from that larger population and should be managed accordingly.

Manuscript accepted 28 October 1997.
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Black drum, *Pogonias cromis*, is the largest member of the family Sciaenidae in the western North Atlantic Ocean. Black drum range in U.S. waters from New England south through Florida and across the northern Gulf of Mexico, with Chesapeake Bay being near the northern end of the breeding range (Welsh and Breder, 1923; Hildebrand and Schroeder, 1928). Black drum support important recreational and commercial fisheries throughout their range in the United States. Their population abundance has been historically greater on the Florida coast than northward (Welsh and Breder, 1923), but the degree of stock unity along the east coast of the United States has not yet been determined.

Black drum is migratory in the Chesapeake Bay region. Frisbie (1961) speculated that juveniles move offshore and southward in the fall. Richards (1973) reported that black drum were absent from marine waters off Virginia during winter. Although occasionally caught inshore during winter, black drum generally move inshore to spawn in spring and offshore to overwinter in the fall. The migratory behavior of this fish complicates interpretation of the biological characteristics of the Atlantic coast fishery.

Proper management of the black drum population depends on knowledge of their basic biology throughout their range, particularly their resilience to harvesting. Yet much is unknown about their adult life history and biology in the Chesapeake Bay region where studies have concentrated on early life history. Initial studies of eggs, larvae, and juveniles (Frisbie, 1961; Joseph et al., 1964; Richards and Castagna, 1970) failed to clarify the geographic extent of the spawning and nursery regions. A recent study by Daniel and Graves (1994) concluded that egg production of black drum had been overestimated because of misindentification and that previously reported egg distributions (Joseph et al., 1964) may be incorrect.

Little work has been directed at adult black drum in the Chesapeake Bay region, aside from general faunal studies like that of Hildebrand and Schroeder (1928), and only one study is recent. Studies of early life history by Frisbie (1961) and Joseph et al. (1964) provide little information that can be used in yield modeling to evaluate resilience to harvest. The only studies that provide information specifically useful for modeling include Richards (1973) and Desfosse (1987), both on age and growth. Desfosse (1987) reported ages of 4–15 years with 10-year-olds predominant in the catch, whereas Richards (1973) estimated

maximum age at 35 years. Unfortunately, these studies relied on scales to age black drum. Furthermore, Beamish and McFarlane (1983) reported that scales were not a reliable hard part to age older fish of many species. Hence, the use of scales for ageing black drum in the Chesapeake Bay region may give unreliable results.

Only one recent study of black drum life history has focused on the Chesapeake Bay region; more work has been done in Florida and Gulf of Mexico waters. Pearson (1929) first described the early life stages for black drum in Texas waters. Egg and larval distributions have been reported (Jannke, 1971; Holt et al., 1985; Ditty, 1986), as well as adult distributions (Cody et al., 1978; Ross et al., 1983). Recent studies, based on otolith ageing, report maximum ages of 43 years in the northern Gulf of Mexico (Beckman et al., 1990) and 58 years off the northeast coast of Florida (Murphy and Taylor, 1989). Although Pearson (1929) described spawning migrations of fish over 80 cm, most young fish show little movement between embayments (Osburn and Matlock, 1984).

This paper describes fundamental biological characteristics of black drum in the Chesapeake Bay region that support stock unity of east coast fish. These data can be used as a basis for yield modeling and evaluation of black drum's resilience to harvest. We present the first otolith-based age determination for Chesapeake Bay black drum, which includes characteristics of catch, growth, and mortality. We compare these life history parameters with those derived from other geographic regions.

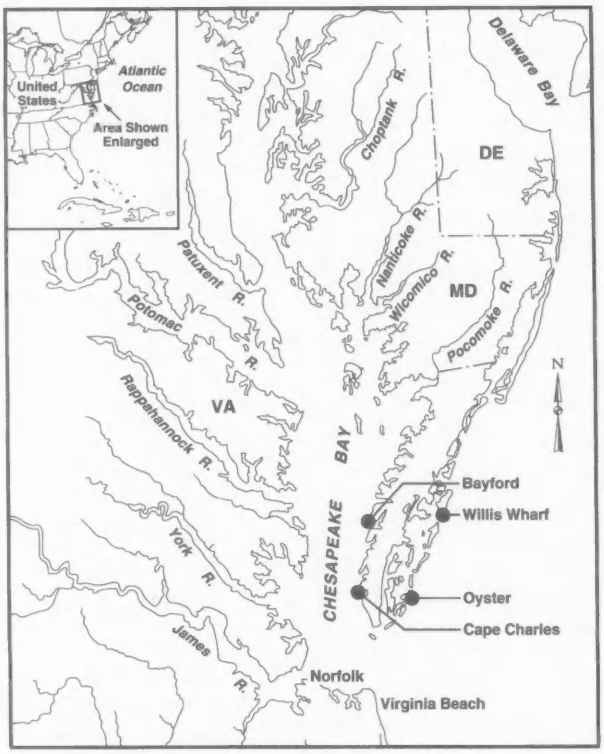

Figure 1
Map of Chesapeake Bay showing Chesapeake Bay region sampling sites.

Methods

Black drum (n=853) were collected March through June, 1990–92, from commercial and recreational fisheries on the eastern shore of Virginia where more than 90% of the catch is landed (Jones et al., 1990). Commercial landing sites were located at Willis Wharf, Oyster, and Bayford; recreational sites were at Cape Charles and Cherrystone Point (Fig. 1). Fishermen were asked for the location of their catches. Collection sites were visited daily once the first landings were made. Additionally, in the fall of 1990 and 1992, we obtained juveniles (n=10) from special sampling of pound nets near the bay mouth.

Fish were sexed and measured for total length (TL), standard length (SL), total weight (TW), gonad weight (GW), girth at the preopercle (G1), and maximum girth (G2). Sagittal otoliths, dorsal spines, and fin rays were taken from each specimen. One otolith, chosen randomly from each pair, was transversely sectioned through the core on a Beuhler low-speed Isomet saw. Three sections of about 300-m thickness were mounted with Flo-texx mounting medium on a slide and read under a dissecting microscope (10×) with transmitted light and bright field. Dorsal spines and fin rays were processed similarly (10–40×) but sectioned perpendicular to the long axis of the growth plane, close to the base. To compare hard parts, we read random sections without knowledge of length or collection date of specimen.

Ages were assigned on the basis of counts of annuli. We call them presumptive annuli in this paper because we have not completed validation of ages 44–59. However, otolith annuli have been validated to age 43 in the Gulf of Mexico through marginal increment analysis (Beckman et al., 1990; Fitzhugh and Beckman[1]), and we have recently shown corre-

[1] Fitzhugh, G. R., and D. W. Beckman. 1987. Age, growth and reproductive biology of black drum in Louisiana waters. Coastal Fisheries Institute, Center for Wetland Resources, Louisiana State University, Final Report of Funded projects FY 1986–1987, 89 p.

spondences between bomb radiocarbon chronologies from the atmosphere and those from otolith cores of black drum (Campana and Jones, 1998). Average birth date was arbitrarily taken to be 1 January (Jearld, 1983). To assess ageing precision, all hard parts (n=30) were read twice by each of two readers, and agreement between and within readers was evaluated by percent agreement methods (Beamish and Fournier, 1981; Chang, 1982). Disagreements were resolved by a third reading.

To evaluate changes in otolith size in relation to fish total length and age, otoliths from 300 fish (1990 collections; ages 0–57; 22.9–130.0 cm TL) were measured for maximum length (otolith length [OL] ±0.01 mm), radius along the sulcal grove (otolith radius [OR] ±0.001 mm), maximum thickness (otolith width [OWID] ±0.01 mm), and weight (otolith weight [OWT] ±0.001 g). Relation between otolith measurements and fish TL and age were evaluated by simple linear regression analysis.

To evaluate growth, observed individual lengths-at-age were fitted to the von Bertalanffy growth function, VBGF (Ricker, 1975), by using nonlinear regression, SAS NLIN procedure DUD method (SAS, 1988). Likewise, individual weights-at-age were fitted to the VBGF. Model parameters were the following: L_∞, the mean asymptotic length; W_∞, the mean asymptotic weight; K and K', respectively; the Brody growth coefficient on length and weight; and t_0 and t'_0, the theoretical age at which the fish would have zero length on length and weight (Ricker, 1975). Growth curve parameters were compared between years and sexes with maximum likelihood ratio tests (Kimura, 1980).

Linear regression was used to determine length-weight relationships for fish ranging from 22.9 to 130.0 cm TL and 0.6 to 49.4 kg TW. Differences between sexes were tested with Rawlings' (1988) tests of homogeneity of slopes and intercepts by using PROC REG in SAS (Littell et al., 1991). The hypothesis of isometric growth (Ricker, 1975) was tested with a t-test.

Instantaneous total annual mortality rates, Z, were estimated from maximum age with Hoenig's pooled regression equation (Hoenig, 1983), by calculating a theoretical total mortality for the entire life span following the reasoning of Royce (1972), and with the regression method, i.e. with a catch curve combining $\log_e$-transformed recreational and commercial abundance data. In the latter method, mortality estimates were based on data from ages 21–43 and 21–59. Younger ages were truncated because the age group at the apex of the catch curve (age 20) may not have been fully recruited to the fishery (Everhart and Youngs, 1981). Older ages were truncated at the first age class (age 44) with fewer than five fish following Chapman and Robson (1960). Data from 1990 to 1992 were combined to minimize effects of variation in year-class strength (Robson and Chapman, 1961). The right limb of the catch curve was tested for deviation from linearity by analysis of variance (ANOVA). Estimates of Z were converted to total annual mortality rates (A=1–e^{-z}; Ricker, 1975).

All statistical analyses were performed with SAS (SAS, 1988). Rejection of the null hypothesis was based on $\alpha = 0.05$, F-tests in ANCOVA were based on type-III sum of squares (Freund et al., 1986), and assumptions of linearity were checked with residual plots (Draper and Smith, 1981). Data were $\log_{10}$-transformed to correct for nonlinearity and heterogeneity of variance when necessary. Log-transformed data are presented in graphs and tables in original units, unless otherwise stated. Variables that could not be normalized were compared with Wilcoxon's two-sample test or a Kruskal-Wallis test for more than two samples, and large-sample approximate z-scores or χ^2 were reported.

Results

Hard part comparisons

All hardparts showed regular, concentric marks that could be interpreted as annuli. However, marks were not equally clear or consistent between all hard parts. Otoliths were the clearest and most precise of the hard parts to interpret. One hundred percent of otoliths, 36.7% of dorsal spines, and 63.7% of fin rays had marks clear enough to read. Between-reader precision was 100% for otoliths, 27.3% for dorsal spines, and 47.4% for fin rays. Compared with otoliths, dorsal spines and fin rays underestimated age; this underestimation worsened with increasing age (Kruskal-Wallis distribution-free multiple comparison test, MSD=15.81, P<0.05). Underageing was especially marked with dorsal spines. On the basis of these results and otolith growth patterns (see next section), we deemed otoliths the clearest, most reliable hard part, and used them for all ageing.

Otolith size relationships to fish size and age

Black drum otoliths continue to increase in size with fish length and age, apparently throughout life. All measures of otolith size—OL, OWT, OR, OWID—were significantly and positively related to fish length and age. Although black drum otoliths continue to increase in size, the relations of various otolith sizes to fish length and age were not consistent. Relations

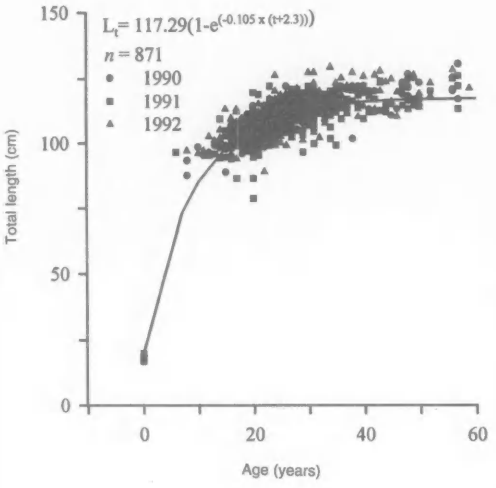

Figure 2

Observed lengths-at-age and fitted von Bertalanffy regression lines for black drum from the Chesapeake Bay region, 1990–92.

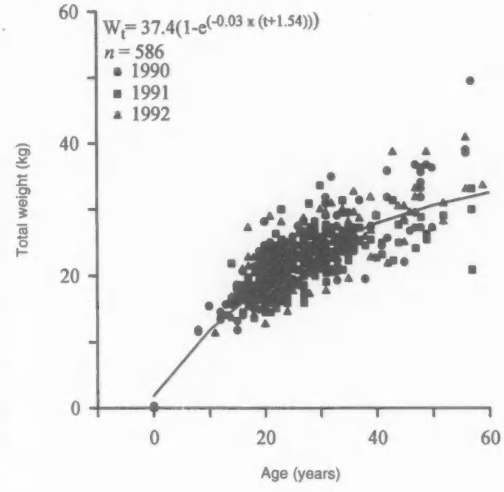

Figure 3

Observed weights-at-age and fitted von Bertalanffy regression line for black drum from the Chesapeake Bay region, 1990–92.

between fish total length and otolith maximum length (OL=2.69 + 0.20TL), and otolith maximum width ($OWID$=2.69 + 0.14TL), were isometric, reasonably linear, and therefore were useful for back-calculation of fish lengths. Other relations between total length and all relations on age were exponential functions (OWT=1.72 × 10^{-5} $TL^{2.66}$; OR=6.02 × $10^{-3}TL^{1.46}$; OL=10.78 $Age^{0.256}$; $OWID$=8.71 $Age^{0.231}$; OWT=0.231 $Age^{0.025}$; OR=0.964 $Age^{0.541}$).

Annuli on black drum otoliths continue to be deposited with increasing fish size. Annuli counts were significantly and positively related to fish length (Fig. 2) and weight (Fig. 3). Fitted regression lines and data plots indicate counts continue to increase most clearly with weight. However, they also increase with length even though there is a leveling off at greater numbers of annuli. Although usually used merely to describe growth patterns, Figures 2 and 3 provide evidence—usually not stated—that otolith age is valid.

Age and size compositions

The Chesapeake Bay fishery generally captures old black drum. Mean age was 26 years (Fig. 4). Ages ranged from 6 to 59 years in the regularly sampled catch, but several juveniles were obtained from sampling pound nets. Median age in the catch was consistent from year to year (1990=25.0, 1991=23.0, 1992=24.0; Kruskal-Wallis χ^2=4.53, P>0.05) and between sexes (♂ = ♀ =24.0; Wilcoxon z=1.01, P>0.05). Age at the 95th percentile was 48 years, indicating that many older fish were landed. The youngest fish

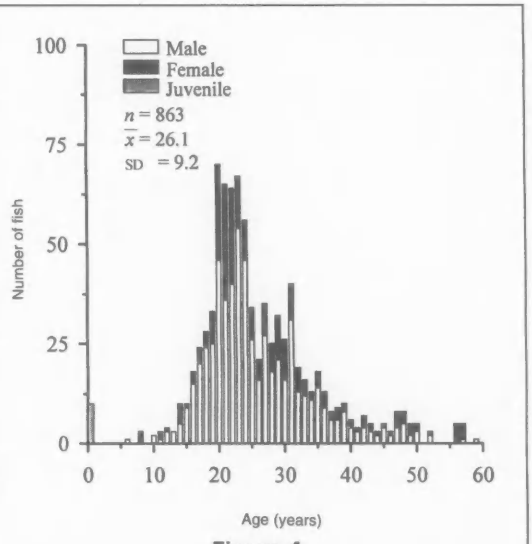

Figure 4

Overall age distribution of black drum in the Chesapeake Bay fishery, 1990–92. Juveniles were taken in the fall of 1990 and 1992 in special sampling of the pound nets.

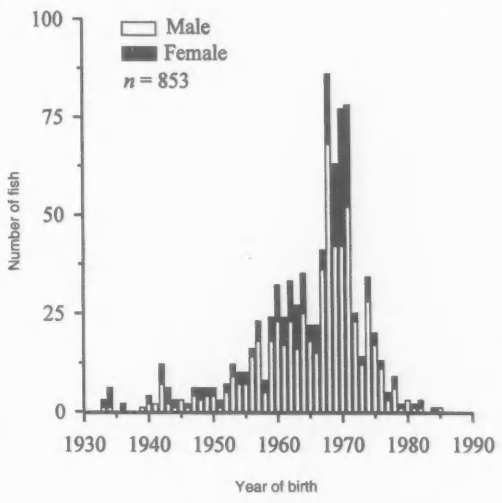

Figure 5

Year class distribution of black drum in the Chesapeake Bay fishery, 1990–92; juveniles excluded.

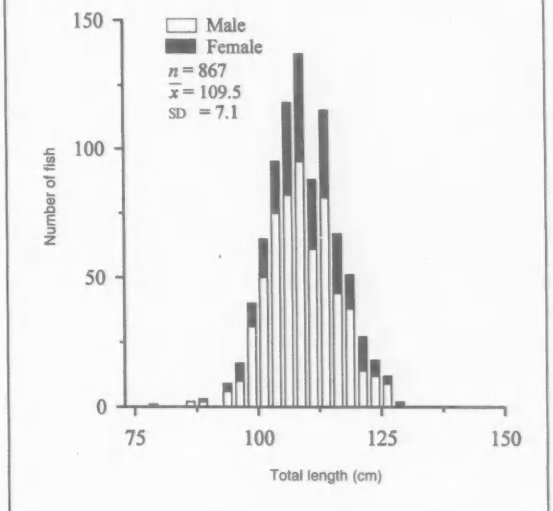

Figure 6

Distribution of total lengths of black drum in the Chesapeake Bay fishery, 1990–92.

caught, apart from young-of-the-year, was age 6, and age at the 5th percentile was 16 years. No fish between 1 and 5 years were found. Recruitment to the gear appears to be complete by age 20 or 21.

Black drum recruitment in Chesapeake Bay is characterized by occasional, dominant year classes (Fig. 5). Exceptionally large year classes occurred in 1934 and 1942, demonstrated in an abundance that fell above the 95% confidence band of expected year class strength around the catch curve. Abundant, but not exceptional, year classes occurred in 1933, 1943, and 1968. Poor year classes, those that fell below the lower 95% confidence interval, occurred in 1939, 1946, 1951, and 1958. We lack information on recruitment after 1972 because black drum are not fully recruited to the bay fishery until age 21.

Total length of adult black drum in Chesapeake Bay averaged 109.5 cm, ranging from 78.7 to 130.2 cm (Fig. 6). Median length (cm) in the catch was not significantly different from year to year (1990=109.2, 1991=108.0, 1992=110.5; Kruskal-Wallis χ^2=4.52, P>0.05), although females were slightly longer than males (♂=109.2, ♀=109.5, Wilcoxon z=2.06, P<0.05). Length at the 95th percentile was 121.9 cm, indicating that many large fish were landed.

Mean total weight of adult black drum in Chesapeake Bay differed slightly between sexes and among years. Total weight of adults averaged 22.1 kg over the period 1990–92 and ranged from 11.3 to 49.4 kg

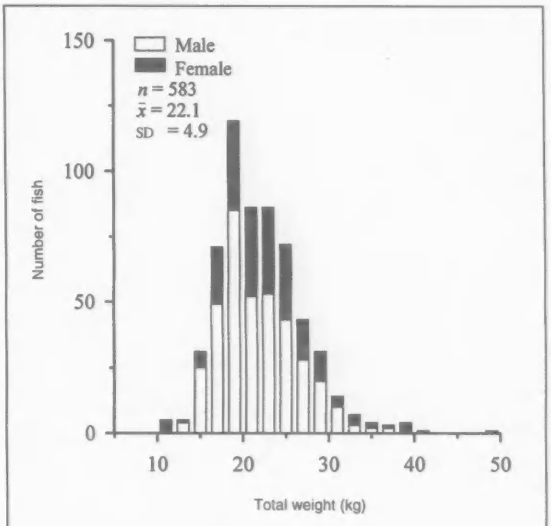

Figure 7

Distribution of total weights of black drum in the Chesapeake Bay fishery, 1990–92.

(Fig. 7). Females were slightly heavier (ANOVA, F=8.23, P<0.05), probably due to their reproductive product. The difference between sexes, 1.1 kg, amounts to only 5% of average total weight. Fish in

1990 (23.0 kg) were slightly heavier (ANOVA, F=4.67, P<0.05) than those landed in 1991 (21.4) and 1992 (22.3 kg). Again, the difference among years is only 7% of average total weight.

Comparisons between areas and gears

Black drum collected in Chesapeake Bay and coastal waters did not differ in simple biological attributes. Catches from the two areas showed no significant differences in age (bay=25.8 yr, coastal=26.8 yr, Z=–1.21, P>0.05), total weight (bay=21.7 kg, coastal=22.4 kg, Z=–1.32, P>0.05), or total length (bay=109.5 cm, coastal=109.5 cm, Z=0.09, P>0.05). Hence, data from both areas were pooled in all other analyses.

Recreational and commercial catches showed statistically significant differences in total length (Z=2.13, P<0.05), but not in total weight (commercial=22.1 kg, recreational=22.2 kg, Z=0.76, P>0.05), or age (commercial=26.3 yr, recreational=26.9 yr, Z=1.60, P>0.05). Mean TL of the commercial catch was 109.0 cm (n=698, SE=8.7 cm), and recreational mean TL was 110.4 cm (n=166, SE=8.6 cm). Mean, median, ranges, and quantile measures of TL are almost identical for these two fisheries. Although the differences in TL are statistically significant because of large sample size, they are not biologically meaningful. Hence, data from these fisheries were pooled to analyze growth and mortality.

Growth

Observed lengths varied greatly within age (Fig. 2). Growth was rapid before 15 years of age but slowed by age 20. Lengths thereafter varied asymptotically about the mean. Black drum have achieved 58% of L_∞, by age 6, when fish are first caught in the bay, and have achieved 90% by age 20, after which they are fully recruited to the gears. Apparently growth was very rapid in the first 5 years, ages absent from our collections. The VBGF equation for data pooled over the period 1990–92 is

$$L_t = 117.3\left(1-e^{-0.105(t+2.3)}\right).$$

No differences were found in growth curve parameters in length between the sexes (P>0.05) or years (P>0.05). We observed large numbers of fish at older age, permitting a good estimate for L_∞ (n=871; includes juveniles, r^2=0.998). However, because we observed no fish between 1 and 5 years, our estimate of K is not optimum. Parameters estimated and asymptotic standard errors are given in Table 1.

Observed weights of Chesapeake Bay black drum varied greatly within age (Fig. 3). As with age-length data, growth was rapid for the first 6 years. Although it slowed thereafter, fish still grew appreciably in weight until growth slowed substantially at 45 yr. Black drum have reached 22% of W_∞ by age 6 when they first appear in the bay as adults, 51% of W_∞ by age 20, and 78% by age 45. Hence, they grew more slowly in weight than in length. The VBGF equation for data pooled over the period 1990–92 is

$$W_t = 37.4\left(1-e^{-0.03(t+1.5)}\right).$$

We observed large numbers of older fish, permitting a good estimate for W_∞ (n= 586, r^2=0.977). However, because we observed no fish between ages 1 and 5, our estimate of K' is not optimum. Parameters estimated, asymptotic standard errors, and 95% confidence intervals are given in Table 1.

Table 1

Summary of parameter estimates for the von Bertalanffy growth equation on total length (cm) and total weight (kg) of Chesapeake Bay region black drum, *Pogonias cromis* (199092).

			95% confidence intervals	
Parameter	Estimate	SE	Lower	Upper
L_∞	117.3	0.4	116.5	118.1
K	0.105	0.003	0.099	0.111
t_0	–2.3	0.2	–2.7	–1.9
W_∞	37.4	1.7	34.0	40.8
K'	0.033	0.003	0.027	0.039
t'_0	–1.5	0.9	–3.3	0.3

No differences were found in weight-growth curve parameters between the sexes (P>0.05). However, pairwise comparisons showed parameters differed between the years 1990 and 1991 (1990: W_∞=57.2 kg, K'=0.018/yr, t'_0=–2.24 yr; 1991: W_∞=29.8 kg, K'=0.052/yr, t'_0=0.06 yr, likelihood ratio test: χ^2= 10.54, P< 0.05). Fish captured in 1991 weighed less at older ages than in 1990 and 1992. We have no explanation for this; causes could be minor, i.e. sampling error, a slightly greater proportion of older fish that had completed spawning in 1992, or perhaps fish that were in worse condition in 1991.

A pooled length-weight regression was developed (Fig. 8) with the equation

$$TW = 1.01 \times 10^{-2}\, TL^{3.11} \qquad (r^2=0.97;\ n=599;\ P<0.01).$$

The slope of the regression line (b=3.11; SE=0.03) was significantly different from 3.00 (t-test; t=3.75; P<0.05), indicating allometric growth.

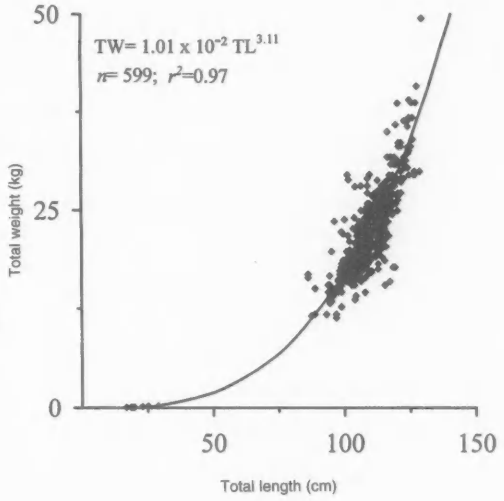

Figure 8

Pooled length-weight relationship of black drum in the Chesapeake Bay region, 1990–92.

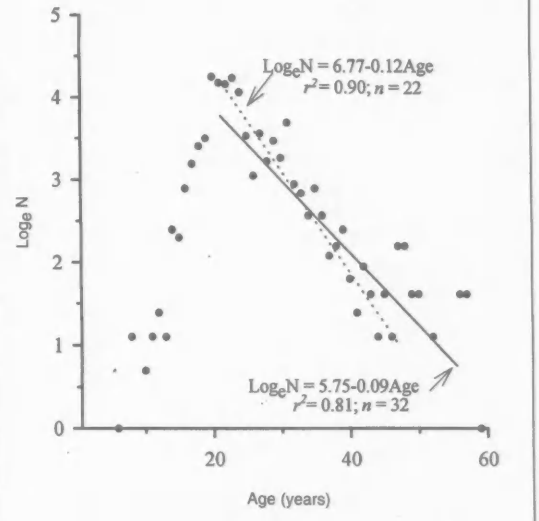

Figure 9

Catch curve for black drum in the Chesapeake Bay region, 1990–92. Fish are not fully recruited to the gears until age 21. Estimates of Z was obtained from fish ages 21–59 (—) and fish ages 21–43 (---).

Mortality

Mean instantaneous total mortality rates, Z, ranged from 0.08 to 0.13. Estimates obtained from a maximum observed age of 59 years, and for age truncated at the 95th percentile—48 years, were 0.08 (A=8%) and 0.09 (A=10%) with Hoenig's (1983) method, and 0.08 (A=8%) and 0.10 (A=10%) with Royce's (1972) method. A regression estimate obtained from the slope of a catch curve truncated at older ages (Fig. 9) was 0.12 (A=13%) with 95% confidence intervals of 0.11 (A=12%) and 0.13 (A= 14%). This regression line did not deviate significantly from linearity (ANOVA; F=1.18; P> 0.05). A regression estimate obtained from the slope of the full catch curve, i.e. with all older cohorts even when n<5, was 0.09 (A=9%) with 95% confidence intervals of 0.08 (A=8%) and 0.09 (A= 10%). This regression line, too, did not deviate significantly from linearity (ANOVA; F=1.29; P> 0.05).

Discussion

Age determination methods

We believe otoliths are the preferred, most reliable hard part to use for ageing black drum. Reasons for this include high precision and readability of otoliths, their continued growth with increase in fish size and age, the increase in the number of annuli with size, and validation over most of the life span. Otolith annuli are extremely clear and easy to read, even out to 59 annuli, and agreement between readings was absolute, 100%. In contrast, fin rays and spines often produced unreadable sections, and fewer bands were counted than on otoliths, especially at older ages.

We have not yet been able to validate black drum otolith ages completely in the Chesapeake Bay region with marginal increments or other analyses. However, evidence from other regions indicate that black drum otoliths are valid throughout much of their life. For example, Fitzhugh and Beckman,[1] and Beckman et al. (1990) used marginal increment analysis to validate otolith annuli formation in black drum to age 43 from Louisiana. However, because most of their fish were age 5 to 27, they had to group the few fish at older ages. Our putative ages extend an additional 15 years beyond the range these authors described. Other evidence indicates members of the family (Sciaenidae) consistently produce annuli throughout life. Beckman et al. (1989) used marginal increment analysis to confirm annulus formation to age 37 in red drum, *Sciaenops ocellatus*. Ross et al. (1995) confirmed annuli formation in two red drum aged 38 and 40 through oxytetracycline marking of otoliths. Although we have not yet fully

validated ages from 44 to 59 years, we have found (see above) that black drum otoliths satisfy the criteria of Van Oosten (1929) for annuli: the number of rings increased with mean size, rings were consistently located on otoliths of different putative ages, and otolith radii correlated highly with putative age.

Although we did not evaluate scales because of their problematic use in ageing, we believe there is direct evidence that they underestimate black drum age in the Chesapeake Bay region. Beamish and McFarlane (1983) documented the tendency of scales to underestimate age, especially at older ages. Richards (1973) and Desfosse (1987) estimated maximum ages for Chesapeake Bay region black drum of only 35 and 10 yr, respectively, using scales. Considering that size composition has not changed over the intervening years (Desfosse, 1987; Hutchinson and Rogers[2]), these ages are much younger than we observed. Richards should have seen maximum ages of at least 41, Desfosse at least 57. We therefore argue against using scales for ageing black drum.

Implications of age structure

Although we had only three years of data, the long lives of black drum allowed our collections to represent a history of recruitment of over 50 years—as was the case with Pereira et al. (1995) for freshwater drum, *Aplodinotus grunniens*. Our data show that recruitment of black drum from the Chesapeake Bay region generally appears to be low, with only occasional strong year classes that persist for many years, for example the 1934 and 1942 cohorts. Moreover, low average recruitment is anticipated for a species with a long reproductive lifespan (20 years at the age of capture), high batch fecundity (1–14 million eggs), and several batches in a spawning season (Wells, 1994), especially when the population remains at low abundance throughout the years.

Our recruitment history of black drum also showed an absence of fish ages 1 to 5, which is consistent since at least the 1960s. There are several possible causes: 1) low abundance of black drum young that is hard to measure, 2) recent complete recruitment failure, 3) gear specificity, and 4) migration southward during this life stage and later northward migration. We review the evidence in support of these alternatives briefly.

Given its demography, this stock should have a low survival rate during the early life stages that is difficult to distinguish from zero. Black drum's potential lifetime production of 60–840 million eggs requires mortalities of at least 10^6 or 10^7 during larval and juvenile stages to maintain stable populations. Hence, the high mortality seen in the field (Cowan et al., 1992) is predictable and is difficult, if not impossible, to differentiate from 100% in the field during early life.

The absence of several year classes in the catch of a fishery could also signify complete recruitment failure. Yet indirect evidence does not support this throughout the east coast range. Frisbie (1961) noted the virtual absence of young black drum in the bay and Richards (1973) stated that "black drum of more than 220 to less than 800 mm in length were not readily available . . .". These observations correspond to cohorts from the late 1950s and 1960s which, seen retrospectively in modern catches, showed normal recruitment levels. Even though fish of the expected size of 1–5 year-olds are not typically seen in the bay, these young fish are not missing from the entire geographic range. Fish ages of 1–4 years are found in bycatch from northeast Florida (Murphy and Taylor, 1989). Hence, examination of the catch argues against complete recruitment failure throughout the stock's range.

Fishing gear and practices used for black drum in Chesapeake Bay target large fish and may exclude small fish. The commercial fishery uses anchored and drifted gill nets with 33-cm stretch mesh, which allow smaller fish to escape. Likewise, recreational anglers use hooks that target large fish. Hence, we can explain some of the absence of smaller fish by gear selectivity in the directed fishery. However, if these fish were present in the bay, we would expect to see them in other fisheries, but fishermen have told us that they have never seen these fish in their gear—gear such as pound nets and gill nets of 7.6–15.2 cm (3–6 inch) stretch mesh that would retain these smaller sizes.

Perhaps the strongest alternative explanation for missing 1–5 year-olds lies in the migratory patterns seen in many sciaenids. Specifically, black drum undergo long-range migration along the coasts of the southeast states. Although black drum have been noted as far north as Canada (Welsh and Breder, 1923; Silverman, 1979), they occur more commonly from Delaware south to Florida. Even in the Chesapeake Bay, however, black drum are not resident year round. Frisbie (1961) suggested a southward migration of young fish from Chesapeake Bay in the fall, and the same pattern of fall emigration of juveniles has been shown for Delaware Bay (Thomas and Smith, 1973). Thereafter, only larger and older fish migrate into the bay in the spring—with few younger than six years. In contrast with the Chesapeake Bay pattern, Murphy and Taylor (1989) found that only 20% of their sample from Florida included fish older than age four. Our adult catch data could be ex-

[2] Hutchinson R., and C. Rogers. 1969. Salt water fishing in Virginia. Dep. Conserv. and Econ. Devel., Richmond, VA, 41 p.

plained by the differential seasonal migration northward of older, larger fish from a population centered farther south, as was first postulated by Welsh and Breder (1923). Finally, two fish tagged in northeast Florida were captured about four months later at the mouth of Chesapeake Bay; thus long-range migrations do occur (Murphy[3]).

In summary, migration and gear selectivity are likely explanations of the age structure of the Chesapeake Bay fishery and the apparent absence of age 1–5 fish in this region. However, given our data, we cannot rule out local recruitment failure. Movement and exchange is supported by similar sizes-at-age in fish from Florida and Chesapeake Bay (Table 2): mean maximum length is 117.2 cm TL for Florida, 117.3 cm TL for Virginia; maximum ages along the east coast are 58 for Florida (Murphy and Taylor, 1989), 46 for Georgia (Music and Pafford, 1984), and 59 for Virginia (this study).

Stock unity

Several lines of evidence suggest that black drum on the U.S. east coast are from a common stock. Fish throughout the area appear to have similar growth. Von Bertalanffy growth function parameters that we estimated for the Chesapeake Bay region (L_∞=117.3 cm; K=0.105/yr; t_0=-2.3 yr) were similar to those that Murphy and Taylor (1989) found in northeast Florida (L_∞=117.2 cm; K=0.124/yr; t_0=–1.29 yr). In contrast, black drum from the Gulf of Mexico grow more quickly, are smaller at age, and have a smaller maximum size (Table 2). Mitochondrial DNA evidence also suggests a common stock in the western North Atlantic Ocean. No significant differences in frequency of mtDNA haplotypes were found in fish taken from Virginia and the east coast of Florida (Gold[4]). However, Atlantic east coast fish differed from those sampled in the northern Gulf of Mexico (Gold et al., 1995). Finally, limited tagging data directly suggest black drum move between Chesapeake Bay and Florida (as noted previously).

Implications of mortality estimates

The long life we found in black drum indicates a low mortality rate for larger fish and a stock that cannot support heavy fishing pressure. Our greatest estimate of instantaneous total mortality, Z, converts to an annual total mortality (A) of less than 13%. As $Z = F + M$, natural mortality must also be less than 13%. Because black drum do not completely recruit to the fishery until age 21 in the Chesapeake Bay region, our estimates of total mortality apply to the period of 21 years ago and earlier. For our estimates to be valid today, fishing mortality on young fish must still be low throughout the stock's range. Values of Z have important implications for management. Stocks with high M generally can withstand the highest fishing mortality because fishing simply takes fish that would otherwise die from natural causes. In contrast, stocks with low M (like black drum) do not have a potential for such "excess" natural mortality that can be diverted into fishing mortality (Gulland, 1983; Murphy and Taylor, 1989).

Life history strategy

Black drum have an unusual life history for a long-lived fish. They achieve a large size quickly—84% of

[3] Murphy, M. D. 1995. Florida Marine Research Institute, Department of Environmental Protection, 100 Eighth Ave. S.E., St. Petersburg, FL 33701. Personal commun.

[4] Gold, J. R. 1995. Center for Biosystematics and Biodiversity, Department of Wildlife and Fisheries Sciences, Texas A&M University, College Station, TX 77843. Personal commun.

Table 2

Estimates of von Bertalanffy growth function parameters from various studies of black drum. Standard errors in parentheses (when available).

Area and study	Growth parameters			Sample size	Total length range (cm)
	L_∞ (cm)	K	t_0		
Atlantic coast					
Murphy and Taylor (1989)	117.2 (0.9)	0.124 (0.003)	–1.29 (0.08)	397	20.2–127.5
Northeast Florida					
Present study	117.3 (0.4)	0.105 (0.003)	–2.3 (0.2)	871	22.9–130.2
Gulf of Mexico					
Doerzbacher et al. (1988), Texas	79.8 (4.2)	0.219 (0.027)	—	383	20.3–99.1
Beckman et al. (1990), Louisiana	110.0	0.038	–16.42	1072	—

their total potential growth is accomplished in only 20% of their life span. Moreover, they become sexually mature at age 5–6 years (Murphy and Taylor, 1989) and appear reproductively active over a potential lifespan of some 60 years. Life history theory indicates that species that have an early age at first reproduction and fast growth tend to be short lived (Begon et al., 1990; Charnov, 1993). Typically, long-lived fishes grow slowly and mature late, like sturgeons (Jenkins and Burkhead, 1993) and redfishes, *Sebastes* (Scott and Scott, 1988; Beverton, 1992). Black drum are as long-lived as these fishes but have faster early growth and a relatively early age of first reproduction. This strategy may give black drum a capacity to maintain population stability greater than that seen in similarly long-lived fishes in the presence of heavy fishing.

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Stock structure and movement of tagged sablefish, *Anoplopoma fimbria*, in offshore northeast Pacific waters and the effects of El Niño-Southern Oscillation on migration and growth

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Abstract.—Sablefish in the northeast Pacific are found in commercial quantities from the Bering Sea, the Aleutian Islands, throughout the Gulf of Alaska, and south along the west coast of Canada and the U.S. to Baja California. Tag-recovery data support a two-population hypothesis throughout the North American range: an Alaska population ranging from the Bering Sea, including the Aleutian Islands and extending down through the Gulf of Alaska to northwest Vancouver Island, Canada; and a west coast population extending from southwest Vancouver Island to Baja California. Tag recoveries indicate that these two populations mix off southwest Vancouver Island and northwest Washington, and to a lesser extent off southern Washington and Oregon.

Alaska sablefish, which commonly migrate over 500 n mi, are more mobile than west coast sablefish. Tag recoveries for sablefish tagged in Alaska have shown strong mutual exchanges between nearly all areas. In contrast, west coast sablefish have shown far less migratory behavior. Tagging data with respect to bathymetry are difficult to interpret in both regions owing to the fact that tagging and recovery effort do not cover the full bathymetric range of adults.

Results of analysis of tag-recapture growth data were consistent with patterns observed for several other pelagic and demersal species. That is, El Niño-Southern Ocean Oscillation events appeared to retard the growth of sablefish along the west coast and to enhance growth of Alaska sablefish. The timing of recoveries from sablefish tagged off Alaska and recovered off southwest Vancouver Island and Washington–Oregon suggests that movement south correlates positively with strong upwelling in this southern area. Although sablefish trap-index surveys show a north to south cline in the percentage of large sablefish (>60 cm, and possibly of Alaska origin) sampled in length frequencies along the west coast, we were unable to correlate annual fluctuations in these percentages with upwelling strength.

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Adult sablefish have a proclivity for great depths (200–1500 m) where the ocean environment is relatively constant over extensive geographic distances and consequently can be found from central Baja California along the Pacific coast through the Gulf of Alaska and Aleutian Islands, along the Bering Sea slope to the Russian coast, and down the Kamchatka Peninsula all the way to southern Japan (OCSEAP, 1986; Allen and Smith, 1988).

The marked absence of sablefish eggs and larvae from the Bering Sea above 55°N is usually attributed to an intolerance to low (<2°C) temperatures (OCSEAP, 1986). Sablefish occurrence in the Bering Sea and Aleutian Islands is thought to be dependent on egg and larval drift from the northeast Pacific, principally through westward transport from the Gulf of Alaska by the Alaskan Stream (OCSEAP, 1986). Although sablefish occur along the coast of Asia, only adult fish (>2 yr) are found (Kodolov, 1968) and they are believed to have been recruited from the northeast Pacific stock. Ocean currents from the western Bering Sea favor dispersal of sablefish along the Asian coast by means of the East Kamchatka and Oyashio Currents.

Commercial catches of sablefish appear to be absent off Japan (Chikuni, 1985). We do not know if commercial catches of sablefish occur off Russia, although Kodolov (1968) describes the adult distribution of sablefish as extending from the Bering Sea all along the Kamchatka Peninsula. In contrast, sablefish is an important commercial species throughout the northeast Pacific with average annual landings (1984–93) of 2150 t for the eastern Bering Sea, 2405 t for the Aleutian Islands, 22,590 t for the Gulf of Alaska, 4835 t for British Columbia, Canada, and 11,129 t for the U.S. West Coast.[1]

Sablefish fecundity is determinate and eggs are spawned in three or four batches (Hunter et al., 1989; Macewicz and Hunter, 1994); eggs are semipelagic (McFarlane and Beamish, 1992) and have been found at depths ranging from 200 to 800 m (Thompson, 1941; Kodolov, 1968; Moser et al. 1994). Age-0 (yr) larvae initially inhabit offshore surface waters (McFarlane and Beamish, 1992), move inshore during the

[1] Aleutian Islands and eastern Bering Sea catches (Lowe, 1995), Gulf of Alaska catches (Fujioka, 1995), Canadian west coast catches (Saunders et al., 1995), U.S. west coast catches (Methot et al., 1994).

summer of their first year (still 0-yr-old) (Rutecki and Varosi, 1997a), and usually become demersal in outer coastal waters during their second year of life at age 1 yr (Rutecki and Varosi, 1997a, 1997b). From there, it is believed that they undergo a protracted ontogenetic migration to greater depths (Saunders et al., 1997).

Adult sablefish recruit to offshore demersal fisheries at about age 3–4 yr (Sasaki, 1985; McFarlane and Saunders, 1997). Routine trawl, longline, and trap surveys by the National Marine Fisheries Service principally cover depths from 200 to 1000 m (Parks and Shaw, 1988; Lauth et al., 1998). These surveys in Alaska, and along the west coast typically indicate sablefish are abundant at the maximum depths fished. Spawning off California occurs at depths beyond 800 m (Hunter et al., 1989). In Monterey Bay, Parrish[2] measured dissolved oxygen and noted that peak longline catches occurred in the oxygen-minimum zone at around 730 m. A special longline survey targeting deeper waters (Wilkins[3]) and deep trap sets (Parks and Shaw, 1988) has shown that sablefish along the west coast occur to depths of up to ~1500 m. Beamish et al. (1979) reported exploratory catches of sablefish to depths of 2740 m. Pearcy et al. (1982) noted the occurrence of sablefish in the Astoria and Cascadia abyssal plains down to a depth of 2560 m. Deepwater trawl and photographic work by Wakefield (1990) showed that sablefish occur as far down as ~1500 m but appear to become scarce beyond this depth. Former naval dumping sites off San Francisco, at depths from 2000 to 3200 m, showed an absence of sablefish (Cailliet et al.[4]). A reasonable interpretation might be that although sablefish can occur at depths beyond 1500 m, sablefish abundance can be expected to decline considerably beyond this depth.

Because of the many interesting questions raised by their broad geographic and bathymetric distributions, sablefish have become one of the most tagged demersal fish species in the northeast Pacific. On the basis of tagging studies, authors have emphasized both the resident nature of some sablefish (Wespestad, 1983; Beamish and McFarlane, 1983, 1988; Maloney and Heifetz, 1997) and the proclivity of other sablefish to be highly migratory (Bracken, 1983; Dark, 1983; Heifetz and Fujioka, 1991; McFarlane and Saunders, 1997). Generally fish tagged inshore, off the west coast of Vancouver Island, or off the U.S. west coast were more likely to be characterized as resident and nonmigratory.

In this paper we examine several hypotheses concerning the movement of sablefish, using recapture data gathered from offshore tagging of sablefish from throughout the northeast Pacific Ocean. The first hypothesis is that sablefish off Alaska and Canada, i.e. north of 50°N latitude, are a separate population from the sablefish south of 50°N latitude found along southern Canada and the U.S. west coast. The second hypothesis is that Alaska sablefish tend to migrate much farther than west coast sablefish. Another question is whether sablefish migrate to greater depths as they become older. Such hypotheses are of practical importance because they can affect the way resource assessment survey results are interpreted.

A study in which growth curves were estimated from a sablefish tag data set has been completed (Kimura et al., 1993). In that study differences in the growth curves of Alaska and west coast populations were reported. In this paper, we examine the effects of El Niño-Southern Oscillation (ENSO) events on the growth of sablefish in the northeast Pacific Ocean.

Finally, we examine the migration of fish tagged in Alaska to areas along the west coast. Upwelling along the west coast (42–48°N latitude) appears to be positively correlated with these migrations, and possible explanations are given for why a correlation exists.

Materials and methods

In this paper we analyze tag recoveries of the sablefish tagging program conducted by the National Marine Fisheries Service (NMFS). Tagging occurred during surveys designed to measure relative abundance of sablefish throughout its range in offshore U.S. waters. From 1971 to 1993, approximately 218,255 fish were captured with trawl, trap, and longline gears and later released after having been tagged with anchor tags (Table 1). With the exception of Canadian waters, sablefish were tagged from southern California to the Bering Sea. Analyses of sablefish tagged in Canadian waters have been previously reported (e.g. Beamish et al. 1979; Beamish and McFarlane, 1983, 1988; McFarlane and Saunders, 1997).

[2] Parrish, R. H. 1975. The relationships of oxygen concentration and depth of capture with size and abundance of sablefish (*Anoplopoma fimbria*) in Monterey Bay, California. Current address: Pacific Fisheries Environmental Lab., 1352 Lighthouse Ave., Pacific Grove, CA 93940. Unpubl. manuscript.

[3] Wilkins, M. E. 1997. RACE Division, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

[4] Cailliet, G. M., W. W. Wakefield, G. Moreno, and K. Rhodes. 1992. The deep-sea fauna from the proposed navy ocean disposal site, using trap, otter and beam trawl, and camera sled samples. Navy CLEAN Contract No. N62474-88-D-5086, prepared for PRC Environmental Management, San Francisco, CA, and Honolulu, HI, 69 p.

From 1971 to 1976, sablefish were tagged and released through a cooperative program involving the NMFS, California Department of Fish and Game, Oregon Department of Fish and Wildlife, and research vessels from Russia and the Republic of Korea. Trawls, traps, and longlines were the predominate gears used to capture sablefish, accounting for approximately 99% of the tag releases.

In Alaska from 1978 to 1993, the U.S.-Japan Cooperative Longline Survey was the primary source of sablefish tag releases; a few releases were made from NMFS trap and trawl surveys. Along the U.S. west coast from 1979 to 1993, most tagged sablefish were released through NMFS sablefish trap index surveys and the remaining fish were released during NMFS trawl surveys.

Tagging from 1971 to 1976 was carried out mainly on the west coast and in southeastern Alaska (Tables 2 and 3). In 1978, tagging operations expanded into the Gulf of Alaska; in 1979, into waters off the Aleutian Islands; and by 1982, into the eastern Bering Sea. Tag releases from 1982 onward has been fairly consistent in all areas.

Table 1

Releases and recoveries by gear and region of release. Also shown are the proportion of recoveries for each combination of gear and region of release. Bottom table shows tag recoveries by gear and region of recovery. Tag types were all anchor tags.

Gear of release	Alaska	West coast	Total
Tag releases by gear and region of release			
Trawl	10,920	28,899	39,819
Trap	7248	30,722	37,970
Longline	136,077	0	136,077
Unknown	4206	183	4389
Total	158,451	59,804	218,255
Tag recoveries by gear and region of release			
Trawl	717	1320	2037
Trap	977	3717	4694
Longline	7987	0	7987
Unknown	166	19	185
Total	9847	5056	14,903
Recovery proportions by gear and region of release			
Trawl	0.0657	0.0457	0.0512
Trap	0.1348	0.1210	0.1236
Longline	0.0587	—	0.0587
Unknown	0.0395	0.1038	0.0422
Total	0.0621	0.0845	0.0683
Tag recoveries by gear and region of recovery			
Trawl	552	1863	2415
Trap	1331	1856	3187
Longline	6342	826	7168
Unknown	1209	603	1812
Total	9434	5148	14,582

Tagging

All sablefish were tagged with anchor tags (Floy FD-68). The vinyl tubing (yellow, orange, or blue) on each tag was 60 mm long, 2 mm in diameter, and bore a unique number and a legend of where to return the tag.

Captured sablefish were routinely put into "live" tanks supplied with fresh running sea water immediately after the catch was brought on board. Anesthetics were not used. Usually within 15 minutes of completion of each haul, sablefish were dipped from

Table 2

We divided the northeast Pacific into 27 areas based on the criteria described below (Fig. 1). The historic regions: eastern Bering Sea (EBS), Aleutian Islands (AI), Gulf of Alaska (GOA), and west coast (WC) essentially maintain their integrity. Nominally, Alaska includes EBS, AI, and the GOA; whereas the west coast includes only WC. Areas are defined in decimal degrees of longitude and latitude.

Area number and region	Area definition	
	Longitude	Latitude
1. EBS	170°E–175°E	Above 55°N
2. EBS	175°E–180°E	Above 55°N
3. EBS	175°W–180°W	Above 55°N
4. EBS	170°W–175°W	Above 55°N
5. EBS	165°W–170°W	Above AK Pen.
6. EBS	160°W–165°W	Above AK Pen.
7. AI	170°E–175°E	50–55°N
8. AI	175°E–180°E	50–55°N
9. AI	175°W–180°W	50–55°N
10. AI	170°W–175°W	50–55°N
11. GOA	165°W–170°W	Below AK Pen.
12. GOA	160°W–165°W	Below AK Pen.
13. GOA	155°W–160°W	Below AK Pen.
14. GOA	150°W–155°W	Below AK Pen.
15. GOA	145°W–150°W	
16. GOA	140°W–145°W	
17. GOA	135°W–140°W	
18. GOA		52.5°N –60°N
19. GOA		50°N–52.5°N
20. WC		47.5°N–50°N
21. WC		45°N–47.5°N
22. WC		42.5°N–45°N
23. WC		40°N–42.5°N
24. WC		37.5°N–40°N
25. WC		35°N–37.5°N
26. WC		32.5°N–35°N
27. WC		30°N–32.5°N

Table 3

Tag releases tabulated by the area of release (rows) and year of release (columns). Areas are described in Table 2 and Fig. 1.

Area of release	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	Total
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	0	0	0	0	0	0	0	0	0	288	181	89	71	167	96	34	102	78	48	12	3	1169
4	0	0	0	0	0	0	0	0	0	0	0	1495	897	549	287	319	370	179	194	113	29	35	5	4472
5	0	0	0	0	0	20	0	0	241	131	288	5070	4488	2642	1823	1594	1025	305	451	264	50	131	20	18,543
6	0	0	0	0	21	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21
7	0	0	0	0	0	0	0	0	0	75	40	82	37	25	33	64	182	70	22	11	19	12	7	679
8	0	0	0	0	0	0	0	0	191	68	101	215	332	283	251	390	450	119	196	31	59	25	9	2720
9	0	0	0	0	0	0	0	0	397	768	1130	1296	701	854	617	775	767	264	410	142	230	136	180	8667
10	0	0	0	0	0	0	0	0	314	307	1071	1015	366	538	526	255	394	126	236	86	33	57	48	5372
11	0	0	0	0	0	0	0	428	414	518	846	1303	863	0	149	148	473	167	190	181	134	104	0	5918
12	0	0	0	0	0	0	0	595	822	780	1466	1380	1532	0	351	370	489	302	503	258	148	226	0	9222
13	0	0	0	0	0	0	0	633	1258	1245	1796	2321	1793	137	476	448	482	824	465	383	180	430	351	13,222
14	0	0	0	0	2	0	0	1702	1820	1984	2133	2120	2166	321	516	380	588	725	607	497	378	511	470	16,920
15	0	0	0	0	34	0	0	693	1060	1938	2703	3316	2301	0	82	0	859	562	201	568	247	452	398	15,414
16	0	0	0	0	67	0	0	705	2112	2574	2462	2257	1340	0	0	0	805	0	0	0	0	0	0	12,322
17	0	0	1523	0	0	34	0	2441	7007	2868	4651	2454	1684	0	0	0	1131	0	0	0	0	0	0	23,793
18	0	2303	5408	0	0	108	0	501	2353	1958	4047	1730	1167	0	0	0	373	49	0	0	0	0	0	19,997
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	446	2046	0	263	0	0	0	802	903	494	0	119	0	102	38	618	0	462	0	0	167	0	6460
21	0	3897	1239	475	448	122	0	0	478	1097	1519	0	524	15	48	205	849	103	810	0	0	364	0	12,193
22	0	4144	1852	541	2259	0	0	0	437	1105	322	0	875	29	0	23	180	17	92	0	0	772	0	12,648
23	0	552	253	260	443	0	0	0	0	0	0	0	464	0	0	1007	0	1670	6	0	811	78	0	5544
24	634	155	0	740	902	0	0	0	0	647	0	763	177	0	0	249	11	968	16	0	93	232	0	5587
25	581	0	0	625	145	0	0	0	0	0	0	0	0	0	0	1106	223	2576	110	0	805	42	0	6213
26	696	0	0	187	270	19	0	0	0	6455	800	475	0	0	0	0	9	0	2	0	0	11	0	8924
27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	363	0	1008	0	0	864	0	0	2235
Total	1911	11,497	12,321	2828	4854	303	0	7698	19,706	25,421	25,869	27,580	22,007	5482	5332	7901	10,374	10,068	5075	2612	4128	3797	1491	218,255

the tank, placed in a padded tagging cradle, measured, tagged, and released. Each anchor tag was inserted between and engaged behind the pterygiophores of the dorsal fin. Fork length, tag number, capture depth, geographical position, and date of release were recorded for each fish. Only fish judged in viable condition were tagged. Sablefish of all sizes (20–110 cm) taken by the capture gear were tagged.

Recovery

A recovery program was promoted through the use of posters, news releases, and letters explaining the research and enlisting the cooperation of those who might encounter tagged sablefish, particularly fishermen, fish processors, and members of state fisheries agencies. Individuals finding a tagged fish were requested to return the tag with information about the date, location, fishing gear, depth of capture, and fish length. A reward and the release history of the tagged fish were provided to those who returned tags.

By the end of 1993, 14,903 recoveries had been made (6.82%). The information garnered from these recoveries constitutes the core of this paper. Owing to the widespread geographic availability of sablefish and the broad coverage of the surveys and fisheries, tagged sablefish were released and recaptured from locations throughout its range in the northeast Pacific Ocean.

Data analysis

Our philosophy in this paper is to present the data as they are and not to adjust the number of tag recoveries for exploitation rates. Such adjustments require knowing the catch and population biomass, or standardized effort measures, by area. If these are incorrectly specified, the data may be further distorted rather than corrected. When the recovery data are being adjusted over an extremely broad geographic range, where dominant gears are different and where even the same gears fish differently, such adjustments become particularly difficult.

Because of the high numbers and long time series of tag returns, basic descriptive tools appear to reveal large-scale migration and stock-structure patterns. Accordingly, we used basic descriptive tools such as mapping locations of tag recovery. Although such visual representations are useful, we also needed to aggregate the data so that general patterns could be more easily discerned. Therefore, we divided the range of sablefish (encompassing the eastern Bering Sea, the Aleutian Islands, Gulf of Alaska, and the west coast of the U.S. and Canada) into 27 areas of moderately small scale. We used large nominal regions (the eastern Bering Sea, the Aleutian Islands, and the Gulf of Alaska) to assist in these demarcations and also a straight line drawn down the Alaska Peninsula passing through 150°W, 60°N and 168.5°W, 53°N and continuing on to 170°W longitude. All areas west of 130°W longitude were divided into areas 5° wide in longitude, and areas east of 130°W longitude were divided into areas 2.5° wide in latitude (Fig. 1; Table 2). The habitat of adult sablefish includes the 400-m depth contour shown in Fig. 1.

Once these areas were described we were able to tabulate the tag recoveries in a table whose rows are the areas of release and whose columns are the areas of recovery. We feel this is the single most useful piece of information that can be garnered from any study of migration based on a tagging experiment. We also characterized net movements by mapping average positions of release and recovery. The average position of tagging and recovery was calculated for all fish tagged in area i, for each area i. An arrow was then drawn from the area of tagging to the area of recovery. The back end of the arrow was in area i, and the position of the arrow point provided some indication of the average movement of the tagged sablefish (i.e. the arrow points to where the tagged fish in area i go). Similarly, the average position of tagged and recovered fish was calculated for all fish recovered in area i, for each area i. The pointed end of these arrows were in area i, and the back end of the arrow gave some indication of where these fish, on average, originated (i.e. the arrow indicated where the tagged fish recovered in area i came from).

Distance traveled was examined by calculating a histogram and empirical cumulative distribution function (cdf) of the distance traveled between tagging and recovery. Movement of tagged fish in relation to depth was examined by simply tabulating the depth of tagging and the depth of recovery.

Modeling ENSO growth effects

Modeling approaches to analyzing ENSO growth effects was difficult because the best model for this apparently simple task was unclear. Assuming an initial size at tagging of S_1, a size at recovery of S_2, and a time at liberty of Δ_t, the most direct model would seem to be something like $S_2 = S_1 + \Delta_t\beta$. However, this model ignores the common sense notions that the growth increment per unit time would be expected to decrease as both S_1 and Δ_t increase and suggests the model $S_2 = S_1 + \Delta_t \exp(\beta_{enso} + \beta_1 S_1 + \beta_2 \Delta_t)$, where β_{enso} represents an ENSO effect, and β_1 and β_2 can be presumed negative. A tagged fish was assumed exposed to ENSO if it was at liberty anytime during a recognized ENSO event: 1972–73, 1976–77, 1982–83, 1986–87, and 1991–93.

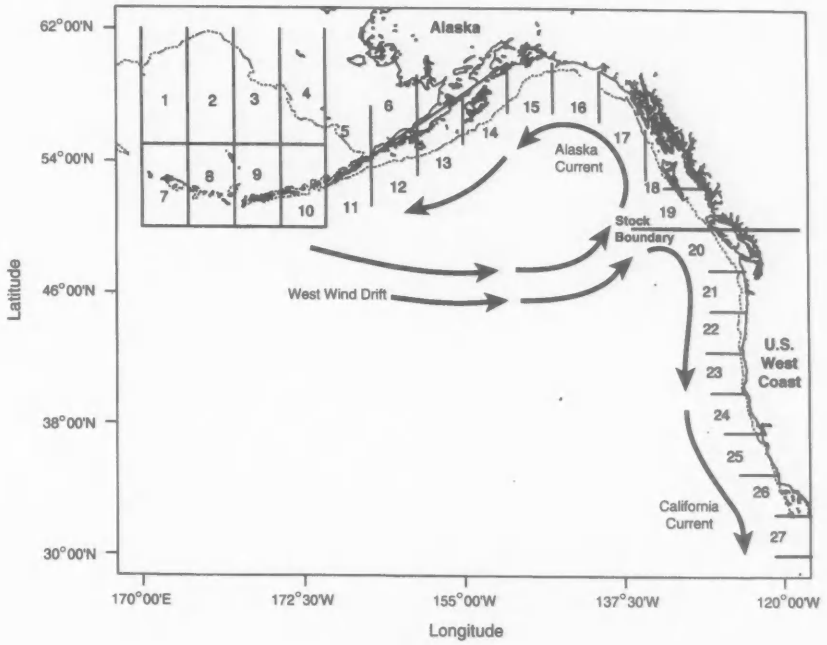

Figure 1

Map of 27 areas (described in Table 2) used in this paper to describe analysis of sablefish tag-recovery data. Principal regions are also described in Table 2. Also shown are the 400-m depth contour, which is the approximate habitat of adult sablefish, and the oceanographic circulation that are hypothesized to affect movements of sablefish.

Migration from Alaska to the west coast

A well-defined sablefish migration seems to occur from Alaska to the northern portion of the west coast. To explore this phenomenon, we plotted the number of tag recoveries from Alaska, recovered along the west coast, against upwelling strength in the northern portion of the west coast. Length frequencies from Alaska and west coast sablefish trap index surveys (Parks and Shaw, 1983) were also used to examine the hypothesis that a substantial mixing of large (>60 cm) sablefish of Alaska origin occurs in west coast sablefish stocks from Vancouver Island and Washington State to California's San Francisco Bay.

Results

Descriptive results

Tag recovery rates by fishing gear type used for initial capture show that the tag recovery rate for trap gear (12.4%) is twice that for longline (5.87%) and trawl (5.12%) gears (Table 1). Because these results hold for fish tagged in Alaska and off the west coast, it is likely that the much higher tag recovery rate for trap gear is due to the superior condition of and presumably lower mortality rate for trap-caught fish.

Tag recovery rates were remarkably consistent for all areas of tagging (Table 4). This finding would suggest that the exploitation rate for sablefish stocks are similar throughout the northeast Pacific. Recovery rates were higher along the west coast (8.4%) than from Alaska waters (6.0%). This is just about the magnitude that would be expected when taking into account the mixtures of gears used for tagging (i.e. if we apply both the recovery rates for trawl and trap caught fish observed from the west coast and the longline recovery rate observed in Alaska to the numbers released in Alaska, we would arrive at the 6% recovery rate that was actually observed in Alaska).

Sablefish are long-lived; ages over 40 yr are regularly documented (Kimura et al., 1993) and a maximum recorded age of 94 yr has been recorded at AFSC (Anderl[5]). The instantaneous natural mortality rate

[5] Anderl, D. M. 1997. Age and Growth Task, Alaska Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE, Seattle, WA 98115. Personal commun.

used for stock assessments is $M = 0.10$ or less (Methot et al., 1994). Thus fish tagged in the early 1970s were still contributing to recoveries as of 1993 (Table 5). It is also notable that sablefish tagged offshore are usually not recaptured immediately; recoveries are typically protracted over many years.

Results related to population structure

Mapping the location of the 14,903 sablefish tag recoveries shows a geographic continuity in sablefish distribution and commercial fishing effort (Fig. 2). The few offshore recoveries in midocean were located on seamounts. If we plot the source of these seamount recoveries (Fig. 3), we see that they came from virtually all areas of release (see Shaw and Parks, 1997, for details).

Table 6 lists the area of release against the area of recovery for the 27 areas in Figure 1. The data show that sablefish tagged off Alaska north of 50°N latitude have a 96.5% chance of being recaptured north of 50°N. Similarly, sablefish tagged off the west coast south of 50°N latitude have a 95.6% chance of being recovered south of 50°N.

Table 6 suggests that Alaska sablefish mix in areas 1–19. It is noteworthy that all Alaska areas show reciprocal migrations to all other Alaska areas. Mixing is also suggested from the fact that the recovery rate for fish tagged in all these areas is similar (Table 4). In contrast, west coast sablefish (areas 20–27) largely confined their movements within the area of release (64.4% of west coast tag recoveries came from the same areas as their release compared with 35.8% for Alaska).

Tag recoveries indicate that Alaska sablefish on average move considerably further than west coast sablefish (Fig. 4). More than 30% of tagged Alaska

Table 4

Table showing the percentage of tags recovered from releases in each area. Also shown by size category are the percentage of tagged fish moving north or west, staying put, and moving east or south. Areas are described in Table 2 and Figure 1.

	All sizes	Size less than 57 cm			Size greater than 57 cm		
Area	Percent recovered	Percent north or west	Percent in area of tagging	Percent east or south	Percent north or west	Percent in area of tagging	Percent east or south
1	—	—	—	—	—	—	—
2	—	—	—	—	—	—	—
3	5.4	0.0	11.8	88.2	0.0	2.2	97.8
4	6.3	0.0	24.4	75.6	0.4	13.0	86.6
5	6.2	2.4	32.7	64.9	1.8	20.9	77.3
6	—	—	—	—	—	—	—
7	3.8	0.0	0.0	100.0	0.0	29.2	70.8
8	5.3	0.0	28.6	71.4	2.9	28.3	68.8
9	5.5	9.1	30.5	60.4	4.1	26.8	69.1
10	5.8	20.0	16.5	63.5	10.6	18.5	70.9
11	6.1	26.6	21.3	52.1	4.8	15.6	79.6
12	6.8	17.4	31.3	51.4	10.5	18.8	70.7
13	5.8	19.3	27.4	53.3	10.9	17.9	71.2
14	5.4	20.5	36.6	42.9	9.8	29.2	61.1
15	4.9	34.9	29.5	35.7	15.2	43.4	41.5
16	4.9	46.4	34.0	19.6	25.9	42.8	31.3
17	6.3	41.9	36.7	21.3	24.2	56.8	19.0
18	7.9	40.9	42.7	16.4	29.2	59.3	11.6
19	—	—	—	—	—	—	—
20	8.0	10.7	74.5	14.8	6.4	76.0	17.6
21	7.6	22.5	66.6	10.9	19.5	71.4	9.1
22	6.0	16.1	73.6	10.4	18.3	70.7	11.0
23	14.8	17.6	64.9	17.5	18.9	67.1	14.0
24	8.4	31.5	61.9	6.6	38.7	55.5	5.9
25	9.1	41.3	54.3	4.5	32.9	64.4	2.7
26	8.8	44.6	54.4	0.9	53.6	46.4	0.0
27	6.7	36.3	63.7	0.0	57.7	42.3	0.0

Table 5

Tag recoveries (1971–93) tabulated by the year of release (rows) and year of recovery (columns).

Year of release	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	Total tag recoveries
71	4	3	1	7	8	2	5	2	6	2	0	0	0	2	0	0	0	0	1	0	0	0	0	43
72	—	72	78	39	114	75	17	31	58	19	29	39	17	6	6	4	6	3	2	0	9	1	0	625
73	—	—	100	85	86	69	23	25	44	49	34	30	14	11	10	9	13	4	12	3	5	10	7	643
74	—	—	—	9	26	16	10	11	11	6	2	1	4	1	3	0	1	0	0	0	2	2	1	106
75	—	—	—	—	49	86	30	22	64	7	21	10	10	11	3	1	3	1	0	0	0	2	3	323
76	—	—	—	—	—	1	0	0	2	0	3	0	1	1	1	2	0	0	0	1	0	0	0	12
77	—	—	—	—	—	—	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
78	—	—	—	—	—	—	—	18	98	50	65	28	37	21	21	13	12	12	3	11	10	13	15	427
79	—	—	—	—	—	—	—	—	116	219	236	160	135	112	96	76	48	59	37	47	40	35	31	1447
80	—	—	—	—	—	—	—	—	—	96	369	296	426	169	131	198	78	90	70	66	57	53	67	2166
81	—	—	—	—	—	—	—	—	—	—	102	310	247	146	173	146	100	101	77	84	74	48	61	1669
82	—	—	—	—	—	—	—	—	—	—	—	71	279	208	255	212	158	168	102	122	92	72	83	1822
83	—	—	—	—	—	—	—	—	—	—	—	—	74	237	279	204	157	152	112	134	89	88	68	1594
84	—	—	—	—	—	—	—	—	—	—	—	—	—	10	39	42	54	59	40	49	27	24	29	373
85	—	—	—	—	—	—	—	—	—	—	—	—	—	—	14	64	56	58	36	39	38	37	35	377
86	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	46	201	155	78	111	69	80	55	795
87	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	43	145	89	93	76	84	76	606
88	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	32	323	262	160	151	60	988
89	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	22	84	81	66	64	317
90	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	35	29	24	92
91	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	48	217	89	354
92	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	17	63	80
93	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	0	0
Total	4	75	179	140	283	249	85	109	399	448	861	945	1244	935	1031	1017	930	1039	1004	1110	912	1029	831	14,859

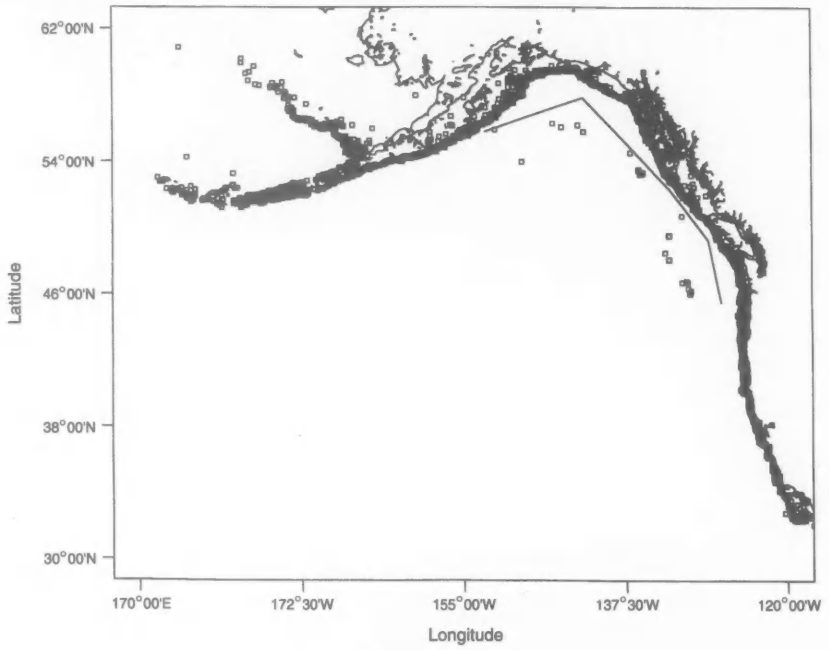

Figure 2

Position of recovery for 14,903 sablefish recovered from 1971 to 1993. Offshore recoveries, separated by line segments, were from seamounts.

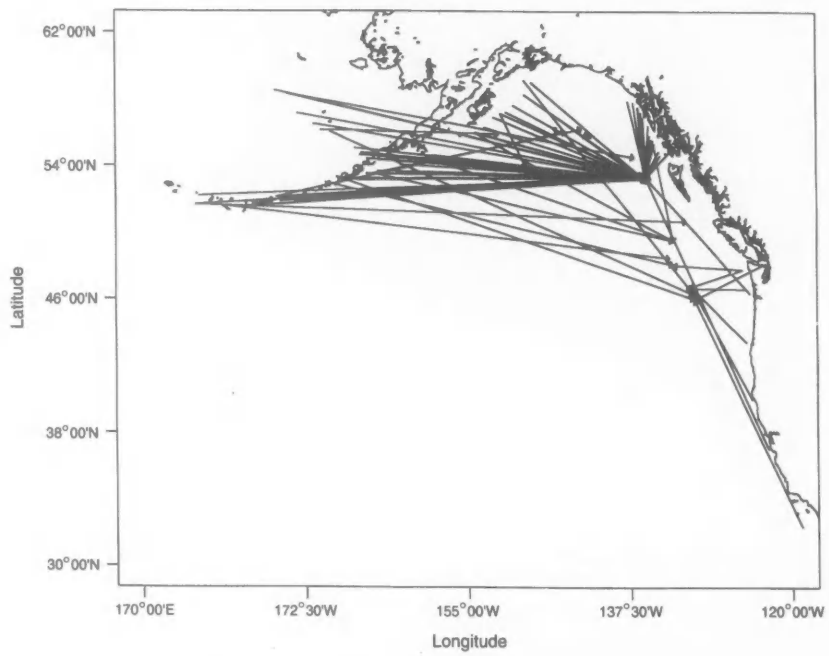

Figure 3

Source of seamount tag recoveries can be seen to be from almost all areas. Figure adapted from Shaw and Parks (1997).

Table 6

Tag recoveries tabulated by the area of release (rows) and area of recovery (columns). Areas are described in Table 2 and Figure 1.

Area of release	Area of recovery																											Total tag recoveries
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	0	0	3	6	5	0	0	1	2	1	1	3	0	1	9	2	16	7	3	2	1	0	0	0	0	0	0	63
4	0	0	1	42	18	1	0	1	8	9	2	8	13	17	46	23	42	29	14	6	1	0	1	1	0	0	0	283
5	0	0	5	18	284	1	2	5	28	19	26	60	46	84	143	115	149	109	39	4	3	3	1	0	2	0	0	1146
6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	0	0	0	0	0	0	7	4	0	1	0	0	1	1	1	2	2	6	0	0	1	0	0	0	0	0	0	26
8	0	0	0	1	1	0	2	41	6	2	3	5	3	6	6	7	28	18	11	3	1	0	1	0	0	0	0	145
9	0	0	0	6	22	0	0	0	134	38	4	13	19	18	36	33	57	50	27	16	3	0	1	1	0	0	0	478
10	0	0	2	4	14	0	1	2	18	56	11	10	10	14	26	24	43	38	25	8	2	0	3	0	1	0	0	312
11	0	0	4	6	16	0	0	2	4	6	62	31	23	20	41	21	50	42	22	8	4	0	1	0	0	0	0	363
12	0	0	2	9	23	0	1	3	9	9	20	136	49	38	78	40	79	63	42	15	6	3	3	0	0	0	0	628
13	0	0	0	5	17	0	0	0	12	12	6	49	157	103	111	56	89	75	41	21	8	1	1	0	0	0	0	764
14	0	0	0	6	17	0	1	2	10	11	10	21	38	284	139	87	114	72	57	24	8	6	2	0	0	0	0	909
15	0	0	1	4	27	0	2	0	4	9	6	12	22	76	297	93	82	57	43	17	8	2	0	0	0	0	0	762
16	0	0	0	1	17	0	0	1	10	10	8	18	26	26	79	241	99	39	19	6	2	0	1	0	0	0	0	603
17	0	0	1	3	26	0	0	4	18	16	13	30	30	60	109	99	796	181	71	27	6	3	2	1	0	0	0	1496
18	1	0	0	1	13	0	0	0	17	6	1	14	13	48	34	54	299	879	115	62	9	8	3	1	1	0	0	1579
19	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0	0	1	1	0	0	0	1	3	1	1	1	6	5	1	6	9	14	387	68	7	2	2	0	1	0	517
21	0	0	0	3	1	0	0	0	0	0	1	3	6	3	10	4	10	11	7	138	638	76	15	2	0	1	0	929
22	0	0	0	0	1	0	0	0	1	1	0	1	2	2	1	2	3	11	5	27	70	548	64	12	2	2	0	755
23	0	0	0	0	1	0	0	0	0	0	1	0	0	5	3	2	2	5	6	6	17	98	534	122	13	2	1	818
24	0	0	0	0	4	0	0	0	0	0	0	2	0	2	2	2	0	3	2	4	11	35	89	282	27	2	1	468
25	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	1	5	1	1	2	8	28	55	123	314	16	8	565
26	0	0	0	0	1	0	0	0	0	1	1	0	2	2	3	0	3	5	7	15	8	57	106	64	84	414	6	779
27	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	4	6	12	15	14	9	13	120	197
Total	1	0	19	116	509	2	16	66	283	210	177	417	461	818	1180	910	1974	1711	572	802	889	887	900	625	453	451	136	14,585

sablefish were observed to move over 500 n mi from tagging to recovery, and more than 10% moved over 1,000 n mi. In contrast fewer than 10% of west coast sablefish moved over 500 n mi.

For the Gulf of Alaska, there is a strong proclivity for fish tagged in the southeast (areas 16–18) to move north and west and for fish tagged in the west (areas 3–14) to move east and south (Tables 4 and 6). It is convenient to define movement north or west as a recovery from an area number less than the area of tagging, and movement east or south as a recovery from an area number greater than the area of tagging (Fig. 1). Several authors (Fujioka et al., 1988; Heifetz and Fujioka, 1991) point out that these directional movements are most pronounced for fish tagged at less then 57 cm in southeast Alaska, and for fish tagged at greater than 57 cm in the western Gulf of Alaska. The greater intensity of these size-selective migrations are supported by our data (Table 4).

The patterns of migration can be illustrated visually by considering maps of average movement where tag recoveries are aggregated by the area of tagging or the area of recovery. Figure 5 shows the average position of tagging (tail of arrow) for each of the 27 areas for which sablefish were tagged (i.e. 23 areas) and the average position where subsequent recoveries occurred. Similarly, Figure 6 shows the average position of recoveries (head of arrow) in each area (i.e. 24 areas) where more than 2 recoveries occurred and the average position of tagging (tail of arrow) for each aggregation of tags.

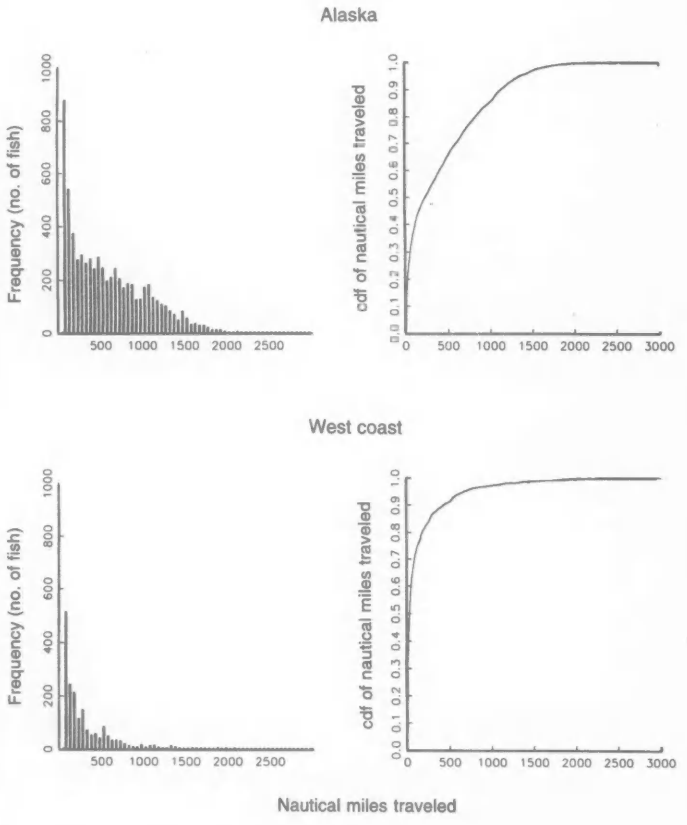

Figure 4

Histogram and cumulative distribution function (cdf) of the distance traveled (n mi) for sablefish that were tagged and recovered. Distances are straight line distances that are minimums; actual distance traveled must have been greater. Histograms are binned in 50 n mi intervals, with the 0–50 n mi bin not plotted so that more detail could be seen. For Alaska the 0–50 n mi bin count was 2744, for the west coast the 0–50 n mi bin count was 3075.

For the Alaska population, Figures 5 and 6 seem to show an expansion and return about the center of sablefish abundance in the central Gulf of Alaska. By this we mean that fish tagged away from the center of the Gulf of Alaska tend to be recovered toward the center of the Gulf, and fish recovered away from the center of the Gulf tend to have originated toward the center of the Gulf. Such a pattern could represent random movement throughout the Alaska range, with concentration of tagging and recovery effort (Tables 3 and 6) occurring in the central Gulf of Alaska. For the west coast population, the movement is more of a slight but steady northward shift whether the aggregation is by area of tagging or area of recovery. Such movement may be the result of migrations or may represent a biologically static situation, one in which recoveries are influenced by increasing fishing pressure towards the north.

As pointed out in the introduction, sablefish inhabit a very broad bathymetry. In order to try to learn something of sablefish depth migrations, we tabulated depth at release for all tagged sablefish and depth at release versus depth at recovery for sablefish that were tagged and recovered (Table 7). Fish that were tagged in Alaska and recovered off the west coast,

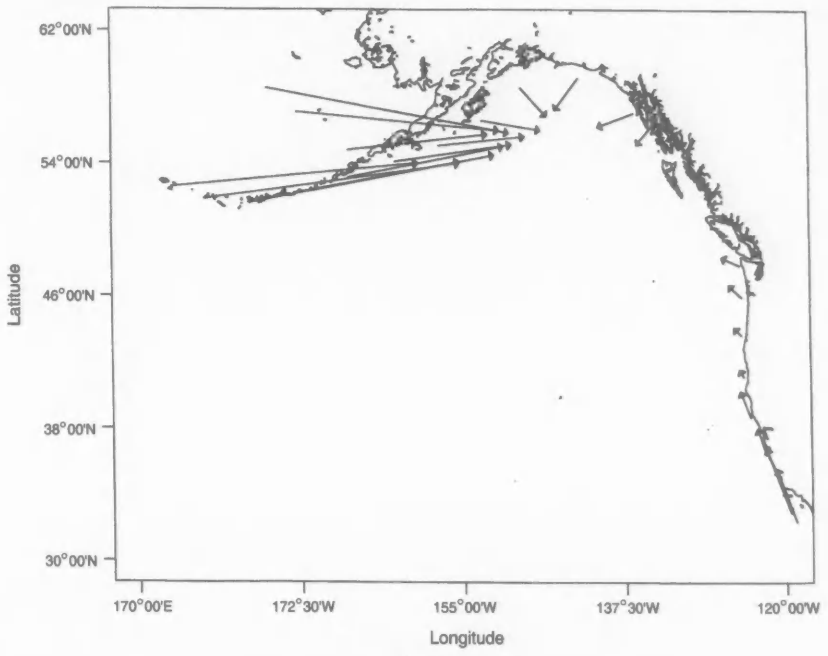

Figure 5

Average movement of tagged and recovered sablefish aggregated by area of tagging. Arrows point to the average location where sablefish tagged in a specified area were recovered (i.e. where fish were going). Tail of arrow originates in one of the 27 areas in which tagging occurred. Tagging did not occur in all areas.

or vice versa, were excluded from Table 7. For Alaska sablefish, the depth of tag recovery generally had the same distribution regardless of the depth of tagging. For west coast sablefish, recoveries tended to be in the same depth zone as the depth of tagging. However, few recoveries were made from the relatively large number of tags released in the 400–1000 m depth zone.

Results related to ENSO events and migration from Alaska to the west coast

Global-scale El Niño-Southern Oscillation (ENSO) events are the strongest climatic feature occurring in the Pacific Ocean. Along the west coast it weakens upwelling and is known to lower food availability and to stunt growth of pelagic species (Bakun, 1996). To the north, off Alaska, ENSO may have the opposite effect, enhancing growth and biological productivity (Beamish and Bouillon, 1993; Bakun, 1996). A significant negative effect on sablefish growth due to ENSO events was detected ($P[|t|>3.973] < 7.2\times10^{-5}$, df=3666) off the west coast, and a significant positive effect on growth was detected ($P[|t|>2.604] < 0.01$, df=6030) for Alaska sablefish (Table 8). In this analysis growth increment data were used only if tagging and recovery occurred in the same region. Residuals histograms suggested a normal pattern of errors for the model fits (Fig. 7).

We found that sablefish that migrate from Alaska waters to the west coast appear to concentrate in areas off Vancouver Island, Washington, and Oregon. Area 20, between 47°30' and 50°N latitude (Fig. 1), is of particular interest because it is an area of mixing for Alaska and west coast sablefish (Table 6, column 20). The question arises whether we can detect factors that might influence the migration from Alaska to areas 20 and 21 off the west coast. One factor that seems to have a positive correlation with this migration south is the strength of upwelling in these southern areas (Fig. 8, two-tailed, sign. $\alpha=0.01$).

Length frequencies from sablefish trap index surveys (1978–91), aggregated over all years, strongly distinguish between fish from Alaska (areas 17 and 18) and the west coast (areas 20–27) (Fig. 9A). However, the length frequencies for fish greater than 60 cm (Fig. 9B) suggest three groups: Alaska (areas 17 and 18), west coast north (areas 20–24), and west coast south (areas 25–27). The west coast north (ar-

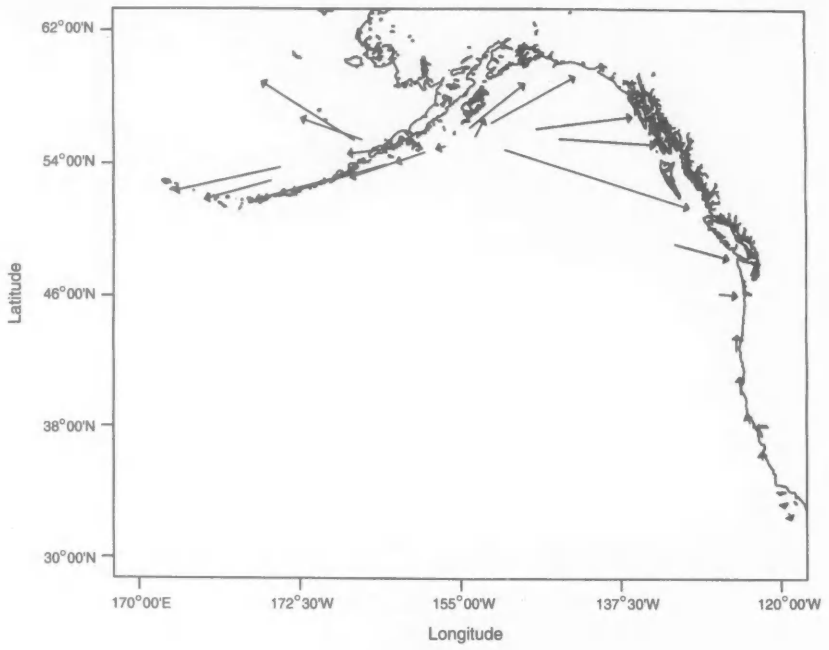

Figure 6

Average movement of tagged and recovered sablefish aggregated by area of recovery. Head of arrow lies in one of the 27 areas in which more than two tag recoveries occurred. Rear of arrows lies in the average location where sablefish were tagged (where fish were coming from).

eas 20–24) group appears to have an excess of large (>60 cm) sablefish, but we cannot be sure of their origin. We were unsuccessful in our attempt to correlate annual fluctuations in the abundance of large sablefish with upwelling, but this may have been due to limitations in the samples that were available on a biennial basis from the west coast north area.

Discussion

Comparison and interaction of Alaska and west coast populations

Our tag-recovery data alone provide compelling evidence (Table 6) that Alaska and west coast sablefish constitute separate populations that, for practical purposes, remain largely independent. In the long-term, approximately 3.5% of Alaska fish migrate to the west coast, and approximately 4.4% of west coast fish migrate to Alaska. Short-term migration rates will be small and justify the separation of these populations for fishery management purposes. However, biologically, these exchange rates are probably sufficient to consider sablefish a single biological population throughout its range, provided these populations are not reproductively isolated. Notice that these migration rates say nothing of net migration which is dependent on the absolute magnitude of the Alaska and west coast populations.

Stock assessment scientists have long felt that sablefish constitute two distinct stocks between Alaska and the U.S. west coast, largely because their von Bertalanffy growth parameters and size-at-maturity differ so dramatically (Table 9; McDevitt, 1990; Kimura et al., 1993). However, early genetic studies (Tsuyuki and Roberts, 1969; Wishard and Aebersold, 1979; Gharrett et al., 1983) indicate that although the northeast Pacific may support many "somewhat discrete" populations, a mechanism for gene transfer was expected to explain the observed polymorphism. In light of our strong evidence for migratory behavior in tagged sablefish, it is not surprising that significant gene flow occurs throughout the range.

The recapture rate for tagged sablefish appears to be remarkably similar for all areas of tagging (Table 4), especially if the differential survival rate from the fishing gears used for initial capture is taken into account. These recapture rates cannot tell us much

Table 7

Number of sablefish tag releases and recoveries by depth category (in meters). Proportions are proportion of total releases that were recovered and the proportion of recoveries that were made at each depth category. Alaska and the west coast was divided at 50°N latitude, with tagging and recovery occurring within the respective regions.

Alaska		Number recovered at depth					
Depth released	Total released	0–200	200–400	400–600	600–800	800–1000	Total recoveries
0–200	11240	75	98	264	237	49	723
200–400	19334	73	365	704	568	116	1826
400–600	108131	51	268	866	856	208	2249
600–800	17572	11	41	206	312	64	634
800–1000	683	2	0	7	31	14	54

Alaska		Number recovered at depth				
Depth released	Proportion recovered	0–200	200–400	400–600	600–800	800–1000
0–200	0.064	0.104	0.136	0.365	0.328	0.068
200–400	0.094	0.040	0.200	0.386	0.311	0.064
400–600	0.021	0.023	0.119	0.385	0.381	0.092
600–800	0.036	0.017	0.065	0.325	0.492	0.101
800–1000	0.079	0.037	0.000	0.130	0.574	0.259

West coast		Number recovered at depth					
Depth released	Total released	0–200	200–400	400–600	600–800	800–1000	Total recoveries
0–200	9208	376	386	34	3	0	799
200–400	15283	309	2054	339	12	0	2714
400–600	23624	6	108	118	7	0	239
600–800	6208	1	5	7	2	0	15
800–1000	4327	0	0	0	0	0	0

West coast		Number recovered at depth				
Depth released	Proportion recovered	0–200	200–400	400–600	600–800	800–1000
0–200	0.086	0.471	0.483	0.043	0.004	0.000
200–400	0.178	0.114	0.757	0.125	0.004	0.000
400–600	0.010	0.025	0.452	0.494	0.029	0.000
600–800	0.002	0.067	0.333	0.467	0.133	0.000
800–1000	0.000	0.000	0.000	0.000	0.000	0.000

about the absolute exploitation rate on sablefish, because tag loss, survival of tagged fish, and reporting rates are unknown. However, the data seem to indicate that the relative exploitation rate of substocks is roughly of similar magnitude throughout their range.

Adult sablefish make two types of migrations that are quite striking in nature: migrations from the continental slope across abyssal plains to seamounts, and long-range migrations along the continental slope that can extend all the way from the Bering Sea to southern California in either direction. The mechanism for accomplishing these long-range migrations has been discussed very little in the literature, although Moser et al. (1994) suggest that migration to seamounts may be midwater over the abyss.

Because adult sablefish are demersal, one possible mechanism for accomplishing these long-range migrations is that sablefish follow the continental slope, or sea floor. Because these deep areas are in the low-oxygen zone (Bakun, 1996), this route would appear

to be a difficult and inefficient for long migrations. Also, it would seem that such migrations would take time, but several authors have noted that for tagged sablefish, there appears to be little relation between time at liberty and distance traveled (Bracken, 1983; Dark, 1983; Beamish and McFarlane, 1988). A second possibility is that sablefish are using the dominant ocean circulation patterns to redistribute themselves.

The dominant circulation patterns in the northeast Pacific—the counter-clockwise Alaska Gyre (and Alaska Current) and the clockwise Central Pacific Gyre (and California Current)—suggest both a physical basis for separation and a mechanism for partial exchanges between Alaska and west coast stocks (Fig. 1). North of 50°N latitude, all life stages of sablefish occur in the counterclockwise rotating gyre. In contrast, south of 50°N latitude, adults live in a northward flowing undercurrent, and pelagic juveniles and benthic subadults live in the southward flowing surface current (i.e. the California Current).

Tag recoveries from midocean seamounts come from all areas of tagging and appear to demonstrate that sablefish routinely migrate on (and mix on) open ocean currents from release areas along the continental slope (Fig. 3). The Alaska Current (and Gyre) could provide a passive means for sablefish to make long migrations throughout the Gulf of Alaska. Similarly, the California Current (flowing offshore and southerly on the surface) and the California Undercurrent (flowing nearshore and northerly at depth) could provide the physical conveyance for sablefish to migrate passively up and down the North American west coast.

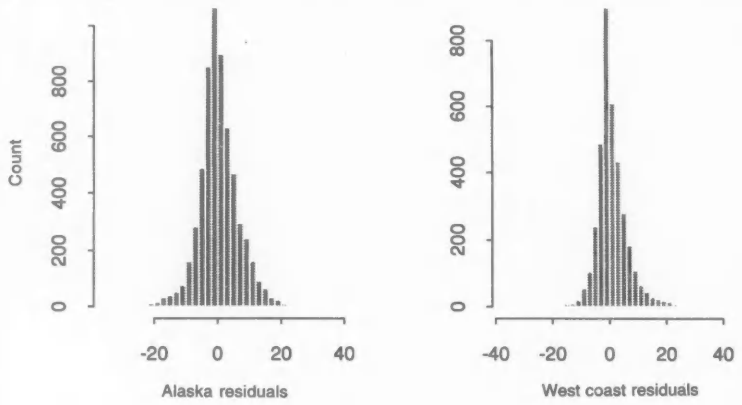

Figure 7

Histograms of residuals from fits to the growth model used to detect ENSO growth effects suggest that residuals from the model fits are approximately normally distributed.

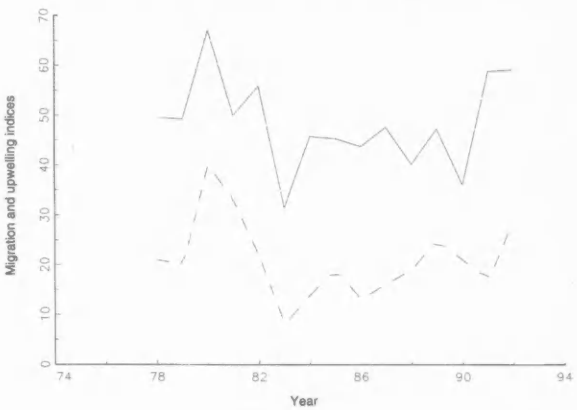

Figure 8

Plot showing correlation of the number of sablefish tagged off Alaska and recovered off the west coast (dash) with the strength of upwelling off the west coast (solid). One year was subtracted from the year of tag recovery, allowing time for the tag recovery to take place. The Bakun upwelling indices were mean coastal summer upwellings (April–August) from 42–48°N latitude (Mason and Bakun, 1986).

Our findings concerning exchanges among areas in Alaska stocks corroborate earlier findings (Sasaki, 1985; Fujioka et al., 1988; Heifetz and Fujioka, 1991). Perhaps the relative strength and general timing of prevailing currents available to Alaska sablefish are what allow them to migrate farther and with greater frequency than west coast sablefish (Fig. 4). The latitudinal range of the Alaska population is only 50–60°N, half that of the west coast population which is 30–50°N. Perhaps this narrower latitudinal range also facilitates migrations.

Earlier, we described how migrations from Alaska to the west coast are reciprocated by migrations from the west coast to Alaska. Although this is true, sablefish

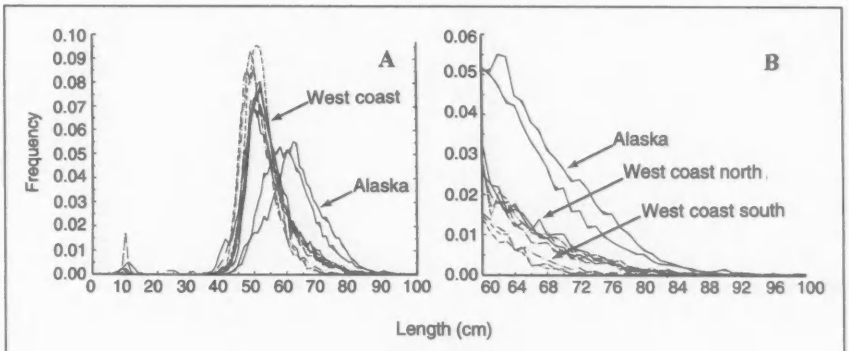

Figure 9

(**A**) Length frequencies from trap index surveys, plotted by areas, showing the dichotomy between Alaska (areas 17 and 18) and west coast (areas 20–27) sablefish. The two distributions shifted to the right are from Alaska. (**B**) The same length frequencies but only for sablefish with length greater than 60 cm. Top distributions are from Alaska (areas 17 and 18), the middle distributions are from the west coast north (areas 20–24), and the lower distributions are from the west coast south (areas 25–27).

migrating from Alaska to the U.S. west coast appear to concentrate in the northern area of the west coast (areas 20–22, Table 6).

Methot[6] recognized from fishery data that west coast sablefish varied greatly in size at age. He suggested that this was due to a commingling of southern California and Alaska "morphs." Extending this hypothesis, tag recoveries (Table 6) suggest that area 20 contains a substantial number of fish from Alaska, but that areas farther south contain substantially fewer migrants. Similarly, length frequencies of large fish from the NMFS trap index survey (Fig. 9B) suggest three populations: Alaska fish from areas 17 and 18; a mixture of Alaska and smaller southern California fish from areas 20–24; and small southern California fish from areas 25–27.

On the basis of size and age-at-depth data, adult sablefish are believed to inhabit greater depths as they grow older owing to a protracted, ontogenetic migration to greater depths (Fujioka et al., 1988; Saunders et al., 1997). Norris (1997) disagreeing with this view, conjectured that the broad bathymetric range was due to radiative evolutionary adaptation of enzyme systems to greater depths. Norris (1997) regarded the age-at-depth data as an artifact caused by varying size-selective fishing mortality with depth. He felt that reproducing populations inhabit various depth zones. Sigler et al. (1997) hypothesized that age-at-depth data could be explained by considering the movement of sablefish to greater depths as being a random walk (i.e. resulting from a sequence of random movements). From this point of view, greater age-at-depth could be viewed as an ontogenetic phenomenon resulting from statistical behavior.

Table 8

Parameter estimates and their statistical significance for a tag-recovery growth model intended to detect a growth effect due to ENSO events. Data were divided between Alaska and the west coast and the ENSO parameter was included when a particular tagged fish was at liberty during any ENSO event. The model used was $S_2 = S_1 + \Delta_t \exp(\beta_{enso} + \beta_1 S_1 + \beta_2 \Delta_t)$, where S_1 was the size of fish at the time of tagging, S_2 was the size of fish at time of recovery, Δ_t was the time elapse between tagging and recovery, and β_{enso} represents an effect from any exposure to ENSO events. Both release and recovery were in the same region for the data used.

Parameter	Estimate	SE	*t*-value
Alaska modeling results.			
Degrees of freedom for *t*–statistic=6,030.			
β_{enso}	0.05781	2.2200×10^{-2}	2.604
β_1	–0.08307	4.8603×10^{-4}	–170.910
β_2	–0.00031	9.9375×10^{-6}	–31.093
West coast modeling results.			
Degrees of freedom for *t*-statistic=3,666.			
β_{enso}	–0.12918	3.2513×10^{-2}	–3.973
β_1	–0.09636	7.4322×10^{-4}	–129.651
β_2	–0.00036	1.4059×10^{-5}	–25.853

[6] Methot, R. D. 1993. Latitudinal and bathymetric patterns in sablefish growth and maturity off the U.S. West coast. Paper presented at the international symposium on the biology and management of sablefish, Alaska Fisheries Science Center, April 13–15, 1993.

Table 9

Von Bertalanffy growth parameters and lengths at maturity for Alaska (AK) and west coast sablefish. Growth parameters are based on age data (Kimura et al., 1993). Lengths at maturity for Alaska are from Sasaki (1985), and for the west coast are from Parks and Shaw (1983).

Region	Location	Sex	L_∞ (cm)	K	t_0 (yr)	Length at maturity (cm)
Alaska		male	70.2	0.120	–8.06	
		female	86.7	0.106	–6.15	
	Bering Sea	male				65
		female				67
	Aleutian Islands	male				61
		female				65
	Gulf of AK	male				57
		female				65
West coast		male	54.7	0.472	–1.82	
		female	61.0	0.499	–0.81	
	Bodega Canyon	male				52.7
		female				55.3
	Patton Escarpment	male				54.8
		female				56.3

Depth-related tagging data for sablefish are very difficult to interpret for several reasons. First of all, surveys, and therefore tag releases, did not cover the full bathymetric distribution of sablefish. Second, commercial fishing, and therefore recovery effort, did not cover the full bathymetric distribution of sablefish. And finally, the bathymetric distribution of a species abundant across such a broad latitudinal range as sablefish, might be expected to vary by latitude.[7] Most of our evidence supports the hypothesis that sablefish seem to have a deeper, lower limit to their distribution off the west coast, compared with their distribution off Alaska.

The principal depth-related result for Alaska sablefish is that the depth distribution of recoveries is similar regardless of the depth of tagging (Table 7). Although the depth distribution of recoveries naturally follows recovery effort, it also suggests a certain amount of random movement in relation to depth over time. The depth-related data for west coast sablefish are even more difficult to decipher. These data show an extremely low recovery rate from fairly heavy tagging of fish from the 400–1000 m depth zone. The reason for this low recovery rate is unknown. Perhaps, the strongest conclusion to emerge from our study is that we still have more to learn about sablefish depth distributions.

Effects of ENSO on migration and growth

It seems natural that the growth of pelagic species off the west coast, such as Pacific whiting (*Merluccius productus*) and Pacific salmon (*Onchorynchus* spp.), would be adversely affected by ENSO events (Beamish and Bouillon, 1993; MacLellan and Saunders, 1995). It is perhaps more interesting that along the west coast, the growth and somatic condition of adult rockfish have been negatively affected by ENSO (Lenarz et al., 1995). That the observed growth of a deepwater species, such as sablefish, can be negatively affected suggests that the feeding of many demersal species along the west coast may suffer some ill effects from ENSO. In the Gulf of Alaska, ENSO growth effects are thought to be opposite of those experienced off the west coast. Growth of salmon and groundfish species are thought to be significantly enhanced by ENSO events (Beamish and Bouillon, 1993; Bakun, 1996). Thus our findings that ENSO events retard growth of sablefish off the west coast but enhance growth of sablefish off Alaska are consistent with this literature. However, this may be the first documentation of this effect for a demersal species.

The question arises as to why there is a positive correlation between Bakun's upwelling index and west coast tag recoveries of Alaska fish (Fig. 8). Are

[7] One reviewer noted the term "latitudinal emergence," where deeper dwelling species are thought to have shallower upper limits on their bathymetric distributions in the more northern limits of their range. However, we did not find this term to be widely used in the literature.

migrating sablefish taking advantage of enhanced feeding opportunities presented by strong upwelling or are they displaced sablefish subject to irregular but recurring episodes of ocean-forcing events and passively entrained in strengthened currents southward?

Dorn (1992) noted two oceanographic phenomena that make west coast waters a highly productive region: coastal upwelling and the advection of cool, zooplankton-rich water from the Alaska Subarctic Gyre. These phenomena could be distinguished (Roesler and Chelton, 1987) and Hollowed and Wooster (1992) have pointed out that they are positively correlated.

Hollowed and Wooster (1992) noted that climate and ocean circulation in the northeast Pacific oscillates between a type-A pattern (i.e. weak Aleutian Low and Gulf of Alaska circulation, intensified California Current, and strong upwelling off the west coast) and type-B ENSO-associated conditions (i.e. intensified winter Aleutian Low and Gulf of Alaska circulation, weak California Current, and weak coastal upwelling). It is the more prevalent type-A scenario, with a strong California Current, that possibly facilitates the migration of sablefish south. Thus, the strength of migration from Alaska to the west coast would be negatively correlated with ENSO events. Dorn (1995) concluded that increased northward movements of Pacific whiting along the west coast during El Niño years were due to intensified northward currents. Whether or not a subset of Alaska sablefish follow enhanced feeding gradients, a strong California Current could deliver them to the west coast.

Because the California Current is a surface current and because there exists a natural boundary between the California Current and the Alaska Gyre, it is somewhat speculative to claim that a strong California Current plays an important role in the migration of Alaska sablefish to the west coast. Nevertheless, Alaska sablefish do make this migration, and the migrations coincide with an enhanced California Current and increased upwelling. It would seem difficult to conclude that these phenomena are totally unrelated.

One difficulty in discussing sablefish migration is that we cannot be sure that the larger fish found along the northern portion of the west coast are of Alaskan origin. A partial explanation could be that the strong upwelling zone from Cape Mendocino to Point Conception in central California, as measured by Ekman transport (Parrish et al. 1981), represents a physical barrier to larger (Alaska?) sablefish. This barrier seems plausible because large sablefish become relatively rare in the length frequencies for the areas where upwelling intensifies. The second part of this theory would tell us whether Alaska sablefish are able to reproduce in waters off Washington and Oregon. It is possible that the gross numbers of Alaska sablefish migrating to the west coast are not substantial enough to affect length frequencies directly but that the numbers may be substantial enough to affect the population genetically over a much broader geographic range. Bakun (1996) argued that the Southern California Bight and the Columbia River Plume offer two locations where fish larvae can survive the disruptions of a strong upwelling environment. These locations may correspond to those for northerly and southerly west coast sablefish populations.

However, Moser et al. (1994) believed that although sexually mature and spawning sablefish are encountered as far south as Baja California, virtually none of their reproductive potential survives below the Southern California Bight and they do not contribute to the standing stock in any meaningful way. They concluded that it is the advection of eggs and larvae from the north that ensures the stability of the population south of Pt. Conception. This hypothesis, that sablefish abundance off the west coast (and particularly California) is dependent on a steady "leakage" of eggs, larvae, or juvenile fish from more northern center(s) of abundance, parallels the hypothesis that Asian stocks are dependent on the migration of adult fish from northern and eastern areas of the Pacific.

Although the appearance of northern fish in the mixed-zone off the Washington–Oregon coast is well established, we cannot yet quantify the net contribution of immigrants. Also, we found little evidence of tagged adult fish migrating from areas north of central California to southern and Baja California. However, this does not preclude Moser et al.'s (1994) conjecture that the southern California population is dependent on eggs and larvae advected from the north. The dependence of sablefish stocks on spawning populations appears not to be well understood.

Acknowledgments

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pressed concerning sablefish biology and movement, it is important for us to state that the conclusions described here are those of the authors.

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Age and growth estimates of the bigeye thresher shark, *Alopias superciliosus*, in northeastern Taiwan waters

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Abstract.—Age and growth of *Alopias superciliosus* in waters off northeastern Taiwan were determined from vertebral band counts on 321 specimens (214 females and 107 males) and verified with a length-frequency analysis of 821 specimens (491 females and 330 males). Growth bands formed once a year according to marginal increment analysis and numbered up to 21 and 20 bands for females and males, respectively. The parameters of von Bertalanffy growth equations estimated from vertebral readings were the following: asymptotic precaudal length (L_∞) = 224.6 cm, growth coefficient (K) = 0.092/yr, age at zero length (t_0) = –4.21 yr for females; and L_∞ = 218.8 cm, K = 0.088/yr, t_0 = –4.24 yr for males. The ages at maturity were estimated to be 12.3–13.4 yr for females, 9–10 yr for males. The largest female aged from vertebrae was 20 yr old, the largest male 19 yr old. Length-frequency analysis supported our vertebral ageing estimates.

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The bigeye thresher shark, *Alopias superciliosus* (Lowe), is circumtropical and subtropical in distribution (Compagno, 1984). It is found over the continental slope around Taiwan and is abundant at depths of 40–100 m in waters off northeastern Taiwan (Fig. 1). Based on daily catch data (1989–1994) from Nan Fan Ao fish market, near Suao, estimates of annual landings of bigeye threshers in number of fish are about 3300, and 220 metric tons (t) in weight, 13% of the total annual shark catch.

Biological information, particularly on reproduction, for bigeye thresher is abundant (Nakamura, 1935; Cadenat, 1956; Bass et al., 1975; Stillwell and Casey, 1976; Gruber and Compagno, 1981; Gilmore, 1983, 1993; Moreno and Moron, 1992; Chen et al., 1997) but little is known about age and growth. Other than Gruber and Compagno's (1981) preliminary estimation on the age and growth of bigeye threshers, no studies have been published. Accurate age structure of stocks is essential for stock assessment and fishery management. This study provides the first information concerning age and growth of bigeye threshers from waters off northeastern Taiwan. Age and growth, from vertebral band counts, were verified with length-frequency analysis.

Materials and methods

Thresher sharks caught in northeastern Taiwan waters by commercial longlines were sampled at Nan Fan Ao fish market, from September 1993 to October 1994.

Precaudal length (PCL), fork length (FL), and total length (TL) (in cm) were measured and weighed at the fish market. Because caudal fins of bigeye thresher sharks are often damaged, PCL is used throughout this paper, unless otherwise noted. After specimens were gutted, a total of 371 (245 females and 126 males) precaudal vertebrae were removed for age determination. Vertebrae located under the first dorsal fin are often used for age determination (Casey et al., 1985; Branstetter and Stiles, 1987; Chen et al., 1990); samples from two specimens (166 cm and 171 cm PCL) were used to compare variations in banding patterns from centra at different locations along the vertebral column. Precaudal vertebrae had the same band counts as those under

the dorsal fin and were used for age analysis in this study because these are the only vertebrae readily available at market.

X-ray radiography (Cailliet et al., 1983; Cailliet, 1990; Joung, 1993) and staining of vertebrae (Stevens, 1975; Casey et al., 1985; Tanaka, 1991; Joung, 1993) are two methods commonly used to enhance the clarity of bands on vertebrae. The silver nitrate technique of Stevens (1975) was tried but no increase in clarity of bands was observed; hence, we did not use the technique. The x-ray method, which is simpler and yields better clarity of bands with a Java video image analysis system, was used.

A Rigaku industrial x-ray apparatus (model: radioflex 90 GSB) with Fuji industrial x-ray film (fine grain and high contrast) was used to take x-radiographs of vertebral centra. Banding patterns in every x-radiograph were counted three times by one of the authors during a three-month period; only those centra whose band counts were the same for at least two of the three readings were accepted for further analysis. Growth bands included fast-growth and slow-growth zones. The radii of each band and vertebrae were measured on a line from the nucleus (notochord) to the outer edge of each band and to the outer margin of each vertebrae with x-radiography and the Java video image analysis system (Fig. 2).

The time of band formation was estimated from monthly change of marginal increment (MI) with the following equation:

$$MI = (R - r_n)/(r_n - r_{n-1}),$$

where R = the vertebral radius; and
r_n and r_{n-1} = radii of the ultimate and penultimate bands, respectively.

In addition, Tanaka and Mizue's (1979) method was used to identify the ultimate band on the basis of the following stages: opaque zone, narrow translucent zone (the width of translucent zone is smaller than half width of opaque zone), and wide translucent zone (the width of translucent zone is larger than half width of opaque zone).

The growth of bigeye thresher sharks was described with the von Bertalanffy growth equation (VBGE) as

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right),$$

where L_t = the length at age t;
L_∞ = the asymptotic length;
K = the growth coefficient; and
t_0 = the theoretical age at zero length.

The parameters of VBGE were estimated from a Walford plot (Walford, 1946).

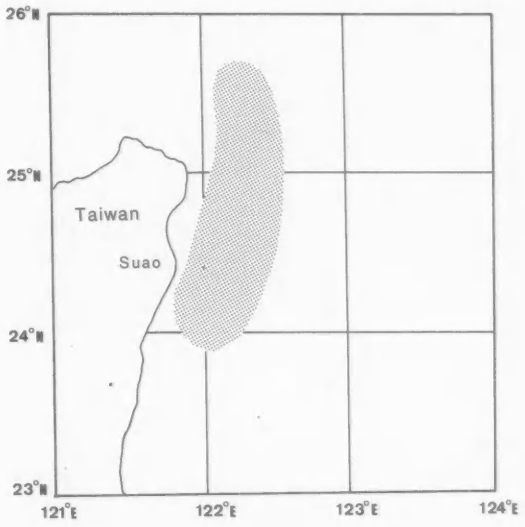

Figure 1

Sampling area for *Alopias superciliosus* in northeastern Taiwan waters.

The asymptotic weight was obtained by substituting L_∞ into the weight-length relationship; the VBGE on weight can be expressed as

$$W_t = W_\infty\left(1 - e^{-K(t-t_0)}\right)^b,$$

where W_t = the weight at age t;
W_∞ = the asymptotic weight; and
b = the exponent of the weight-length relationship.

Length-frequency distributions of 821 individuals (330 males, 491 females), grouped by season and sex, were analyzed with the computer package MULTIFAN (Fournier et al., 1990) to estimate the parameters of von Bertalanffy growth equations. Initial values of the L_∞ and K were adapted from those obtained in the previous section.

The relation between precaudal length and vertebral radius was tested with an F-test, and the difference in regression lines between sexes was tested with analysis of covariance.

Results

The relation between precaudal length and vertebral radius showed a slightly curved trend for both sexes (Fig. 3) and was statistically significant ($P<0.05$).

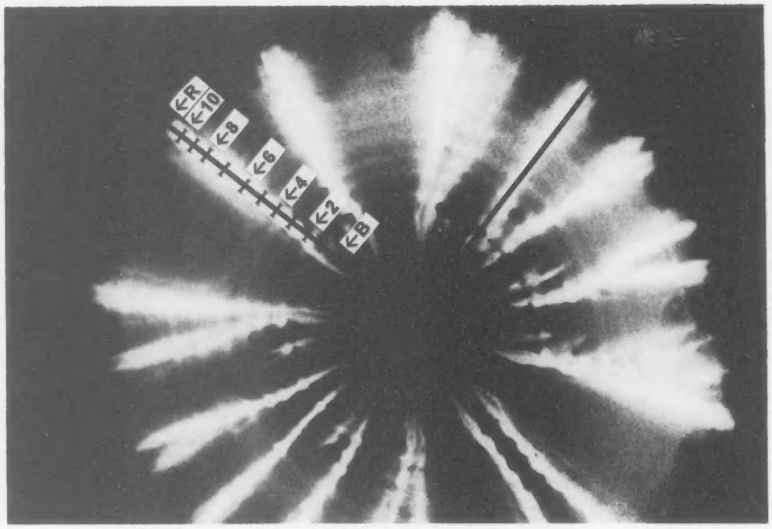

Figure 2

X-ray radiograph of *Alopias superciliosus* used for age determination. B = birth mark, R = vertebral centrum radius. Radiating bands are indicated in even years: 2,4,6,8, and 10.

Analysis of covariance indicated that there is significant difference in PCL-R relationships between female and male ($P<0.05$). Therefore, the PCL-R relationships were expressed by sex as follows:

female: $PCL = 50.84\ R^{0.494}$ (r^2=0.75, n=214),
male: $PCL = 48.91\ R^{0.492}$ (r^2=0.75, n=107).

Growth bands included two types of growth zones, as shown on the x-radiographs. These varied with season; usually a more calcified zone (translucent zones in Fig. 2) represented growth in summer (Casey et al., 1985; Cailliet et al., 1986; Branstetter and McEachran, 1986).

The vertebral bands numbered up to 21 and 20 for females and males, respectively. Owing to a lack of smaller specimens, the mean vertebral radii of bands I–III for females and I–V for males were interpolated from the relationship between vertebral radius and number of bands. The back-calculated length at band formation was able to be obtained by substituting the mean band radii (r_i) for R in the PCL-R relationship (Table 1).

The monthly change in vertebrae (MI) indicated that MI reached its peak in February, 0.60 for males, decreasing thereafter to its lowest value of 0.08 in June, and increasing thereafter (Fig. 4). This trend suggested that a vertebral band was formed once a year

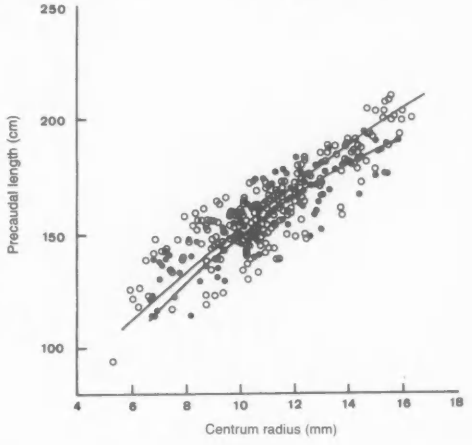

Figure 3

Relationship between precaudal length and centrum radius of *Alopias superciliosus*. ○ = female; ● = male.

in the period April to July. A similar trend was found for females. Following Tanaka and Mizue's (1979) ageing criteria, we found that translucent zones (fast-growth zones) were formed between late spring and early summer, slow growth zones in winter, compa-

Table 1

Back-calculated precaudal length at time of band formation of female *Alopias superciliosus*. *n* = sample size, B = birth.

		Precaudal length (mm)																				
Annulus	*n*	B	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
B	0	793.26																				
1	0	786.92	927.03																			
2	0	780.53	921.27	1075.37																		
3	1	752.31	920.31	1054.06	1153.59																	
4	3	769.59	910.14	1045.81	1146.52	1246.83																
5	8	759.50	877.17	1009.42	1152.07	1239.09	1322.33															
6	5	729.61	891.97	1023.99	1131.02	1232.82	1317.7	1396.33														
7	6	744.71	869.95	996.40	1146.30	1224.89	1310.77	1384.95	1463.29													
8	9	731.17	877.45	1024.23	1116.53	1210.93	1304.95	1378.55	1457.49	1532.69												
9	11	722.11	846.30	1006.05	1109.22	1212.38	1311.24	1372.12	1470.92	1526.92	1590.91											
10	18	705.61	862.39	987.33	1054.89	1205.66	1272.9	1365.65	1445.58	1521.05	1585.60	1643.49										
11	24	688.53	854.31	993.75	1110.68	1199.21	1286.75	1360.44	1418.36	1502.87	1580.65	1637.89	1683.24									
12	30	698.58	848.83	966.57	1089.96	1208.97	1166.43	1377.01	1420.21	1509.31	1567.64	1632.73	1684.05	1742.22								
13	23	657.63	821.34	981.02	1083.27	1189.05	1275.83	1349.21	1429.56	1520.97	1552.99	1612.15	1678.74	1737.38	1788.94							
14	24	691.83	838.97	976.53	1078.4	1151.75	1270.93	1344.77	1423.62	1499.39	1563.67	1622.13	1658.14	1719.16	1783.74	1832.89						
15	15	662.44	835.66	998.03	1074.09	1179.65	1259.09	1340.22	1419.59	1481.62	1559.21	1617.77	1667.62	1726.93	1778.81	1828.50	1870.77					
16	12	684.65	856.08	972.02	1088.92	1211.65	1262.65	1335.28	1410.00	1490.49	1570.17	1598.93	1662.70	1721.47	1789.36	1823.89	1865.81	1909.11				
17	9	700.93	829.29	966.96	1068.47	1171.35	1258.29	1315.52	1410.53	1486.23	1551.14	1608.45	1672.07	1717.29	1769.03	1818.86	1853.57	1904.25	1942.43			
18	10	680.38	827.47	964.23	1064.71	1169.11	1254.72	1326.47	1355.76	1481.87	1546.01	1603.51	1653.05	1712.52	1764.76	1829.31	1856.97	1899.38	1938.22	1966.23		
19	4	679.26	826.40	962.66	1062.00	1166.32	1252.12	1323.27	1402.74	1479.18	1542.23	1599.86	1649.74	1707.81	1760.82	1810.20	1852.30	1894.68	1933.50	1961.51	1981.34	
20	2	673.64	823.19	960.05	1058.21	1164.93	1252.12	1321.1	1401.32	1473.79	1538.35	1595.59	1646.88	1707.01	1759.62	1803.90	1822.67	1893.05	1931.90	1960.12	1980.59	2000.57
Weighted mean		696.35	848.46	985.32	1091.31	1195.33	1263.12	1355.48	1424.73	1504.99	1566.75	1622.46	1671.66	1727.71	1780.21	1826.51	1860.72	1902.87	1938.47	1964.29	1981.09	2000.57
SE		39.856	32.496	28.911	32.895	26.464	36.926	23.599	28.463	18.368	15.378	14.530	12.983	10.142	11.720	10.257	16.303	5.045	3.288	0.980	0.529	0.000

rable to the results from MI. This finding indicates that one band is formed per year by bigeye thresher sharks.

Chen et al. (1997) estimated PCL at birth for the bigeye thresher shark to be 73.7 cm, similar to our estimated mean length at the birth mark formation (69.6 cm). Because no growth band was found for embryos, the first band was assumed to be a birth mark.

For comparison with other literature that reported total length (TL), PCL and FL can be converted to TL with the following equations:

female: $TL = 15.3 + 1.81PCL$ (r^2=0.90, n=177);
$TL = 13.3 + 1.69FL$ (r^2=0.89, n=177);
male: $TL = 15.1 + 1.76PCL$ (r^2=0.88, n=68);
$TL = 26.3 + 1.56FL$ (r^2=0.81, n=68).

The relations between body weight and total length, and body weight and precaudal length are described as follows:

female: $W = 6.87 \times 10^{-5} PCL^{2.769}$ (r^2=0.88, n=421);
$W = 1.02 \times 10^{-5} TL^{2.78}$ (r^2=0.90, n=175);

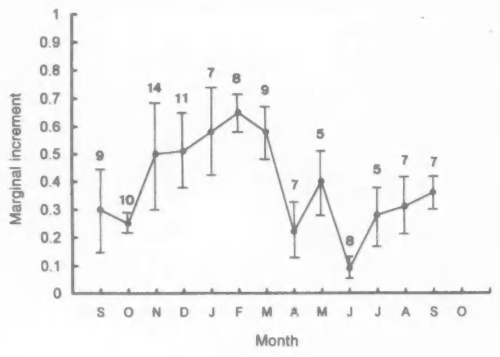

Figure 4

Monthly change of marginal increment of male *Alopias superciliosus*. Numbers indicate sample size and vertical bars indicate ±SE.

male: $W = 9.93 \times 10^{-5} PCL^{2.685}$ (r^2=0.83, n=187);
$W = 3.73 \times 10^{-5} TL^{2.57}$ (r^2=0.80, n=65).

The parameters of VBGE estimated from band counts for females and males are given in Table 2 and the VBGE in PCL (cm) are

female: $L_t = 224.6\ (1 - e^{-0.092(t+4.21)})$;
male: $L_t = 218.8\ (1 - e^{-0.088(t+4.24)})$ (Figs. 5, 6).

With the above equations, the asymptotic PCL can be converted to asymptotic TL as 422 cm for female, 385 cm for male. The VBGE in weight (kg) can be expressed as follows:

female: $W_t = 222.8\ (1-e^{-0.092(t+4.21)})^{2.769}$;
male: $W_t = 190.5\ (1-e^{-0.088(t+4.24)})^{2.685}$.

Female bigeye threshers are estimated to mature between 175 and 180 cm PCL (Chen et al., 1997), 78% and 80% of asymptotic length, and between 12.3 and 13.4 yr old. The largest immature female was 185 cm PCL, 14.6 yr.; the smallest mature female was 154 cm PCL, 8.4 yr. Males mature between 150 and 155 cm PCL (Chen et al., 1997), 69% and 70% of asymptotic length, and between 9 and 10 yr old. The largest immature male was 171 cm PCL, 13 yr; the smallest mature male was 138 PCL, 7 yr (Chen et al., 1997).

The length-frequency histograms for both sexes used in the analysis and results of the best data fits were plotted in Figures 7 and 8, females and males, respectively. In the best fits, age classes 18 and 20 were obtained for females and males, respectively. The estimated modes followed the length-frequency line closely and overlay the peaks well (Figs. 7 and 8). For estimated mean lengths at age of female and males see Table 3. The parameters of VBGE were estimated as L_∞ = 230.5 cm, K = 0.092/yr, t_0 = –3.69 for females, and L_∞ = 224.4 cm, K = 0.087/yr, t_0 = –4.61 for males; these parameters were similar to those from vertebral band counts (Table 2).

Table 2

Comparison of the von Bertalanffy parameters derived from vertebral band count and length-frequency analysis of *Alopias superciliosus*.

	Male				Female			
Parameters	L_∞	K	t_0	n	L_∞	K	t_0	n
Vertebral reading	218.8	0.088	–4.24	107	224.6	0.092	–4.21	214
Length-frequency	224.4	0.087	–4.61	330	230.5	0.092	–3.69	491

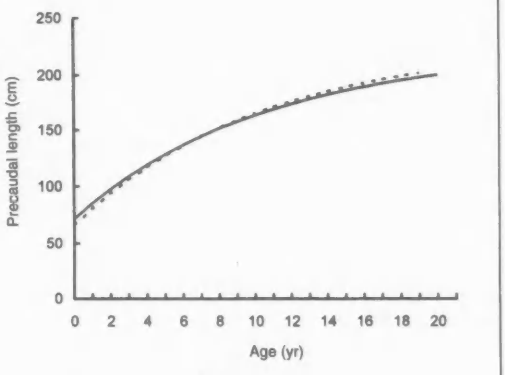

Figure 5

The von Bertalanffy growth curve for female *Alopias superciliosus*. (— = vertebral reading, --- = length frequency.

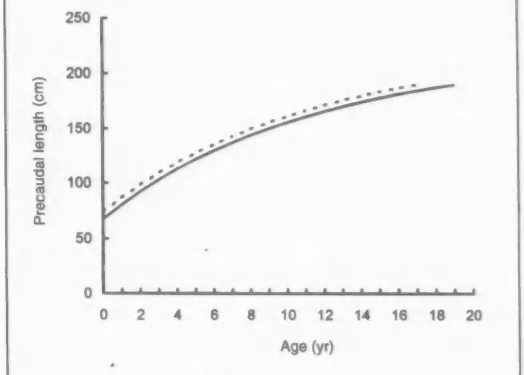

Figure 6

The von Bertalanffy growth curve for *male Alopias superciliosus*. (— = vertebral reading, --- = length frequency.

Discussion

Joung (1993) noted that the ultimate band shown on the x-radiograph was difficult to read with a magnifier. In our study, an image processing system was used to solve this problem.

According to Branstetter (1990), growth coefficients (K) in VBGEs falling in the range of 0.05–0.10/yr is a slow-growing species; 0.1–0.2/yr is a moderate-growing species; and 0.2–0.5/yr is a fast-growing species. In this study, K was estimated as 0.092/yr for females, 0.088/yr for males; these are in the slow-growth category. Cailliet et al. (1983) estimated the growth rate of the California common thresher shark (*Alopias vulpinus*) to be 0.108/yr, comparable to our study. Other slow-growing species include the great white shark (*Carcharodon carcharias*) (K=0.058/yr, Cailliet et al., 1986), bull shark (*Carcharhinus leucas*)(K=0.039/yr, Hoenig, 1979), dusky shark (*C. obscurus*) (K=0.038–0.039/yr, Natanson et al., 1995), sandbar shark (*C. plumbeus*) (K=0.046/yr, Casey and Natanson, 1992, K=0.057–0.089/yr, Sminkey and Musick, 1995), scalloped hammerhead (*Sphyrna lewini*) (K=0.054/yr, Hoenig, 1979; K=0.073/yr, Branstetter, 1987), and *Squalus acanthias* (K=0.037/yr, Jones and Geen, 1977).

Most sharks form a vertebral band once each year i.e. *Triakis semifasciata* (Smith, 1984), *Carcharhinus limbatus*, *C. brevipinus* (Branstetter, 1987), *C. plumbeus* (Casey and Natanson, 1992), *C. falciformis*, *Rhizoprionodon terraenovae*, *Galeocerdo cuvieri* (Branstetter and Stiles, 1987), and *Carcharodon carcharias* (Cailliet et al., 1986). Some sharks form two vertebral bands per year, i.e. *Sphyrna lewini* (Chen et al., 1990), *Galeorhinus japonicus* (Tanaka and Mizue, 1978), *Isurus oxyrinchus* (Pratt and Casey, 1983), and *Cetorhinus maximus* (Parker and Stott, 1965). In the present study, although the time of band formation fell within a greater time range, the hypothesis of one band per year was validated by MI and Tanaka and Mizue's (1979) method. Similar results were reported for other species in Alopiidae, i.e. the common thresher sharks (Cailliet et al., 1983) and pelagic thresher sharks (Liao, 1996).

Formation of shark vertebral bands may be related to water temperature, change of prey (Steven, 1975), shark migration, and mating (Pratt and Casey, 1983). Because bigeye thresher sharks have no fixed spawning season, the band formation may not be closely related to mating. Elevated water temperatures in spring and summer are a possible factor in band formation. Jones and Geen (1977) documented that highly calcified bands represent summer growth of vertebral centra. The first vertebral band was assumed to be a birth mark in this study. Similar findings were reported for other species in Alopiidae, i.e. the common thresher sharks, *Alopias vulpinus*, (Cailliet et al., 1983) and pelagic thresher sharks, *A. pelagicus*, (Liao, 1996).

In the present study, ages at maturity were estimated to be 12.3–13.4 yr for females (332–341 cm TL), and 9–10 yr for males (270–288 cm TL). However, Gruber and Compagno (1981) reported younger ages at maturity but similar sizes in the Atlantic Ocean, 4.5 yr (356 cm TL) and 3.5 yr, females and males, respectively. Gruber and Compagno (1981) counted vertebral bands of a 287-cm-TL female and reported 8–11 bands, 2^+ yr. This length falls in the

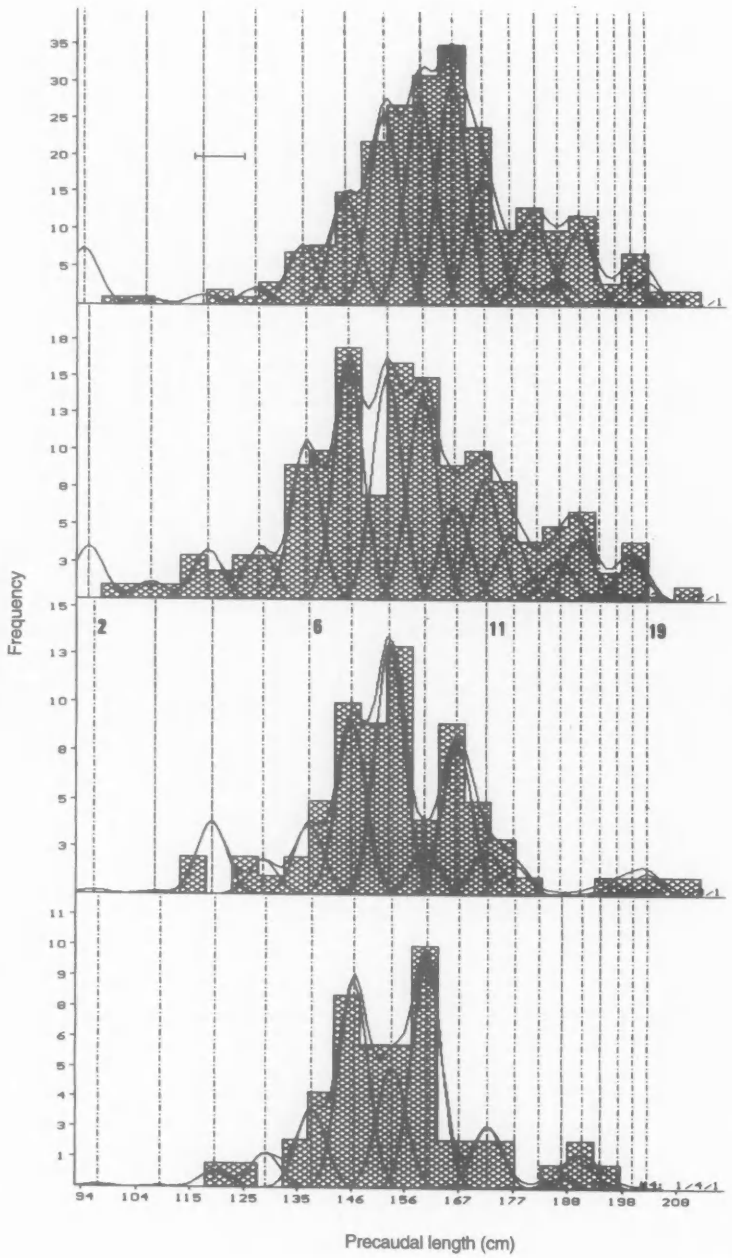

Figure 7

Length-frequency histograms for female *Alopias superciliosus* used in the analysis, and results of the best data fits. Horizontal bars indicate the constraints imposed to mean length at age.

Table 3

Length (cm) at age estimates (yr) from length-frequency analysis of *Alpias superciliosus*. B = birth.

Sex	Age (yr)																		
	B	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Female	66.26	80.71	93.88	105.89	116.85	126.84	135.96	144.27	151.86	158.77	165.20	170.83	176.08	180.87	185.23	198.21	192.85	196.16	199.18	201.93
Male	74.12	86.68	98.19	108.75	118.42	127.28	135.40	142.84	149.66	155.91	161.64	166.89	171.70	176.11	180.15	183.86	187.25	190.36		

9–10 yr age class according to our estimations. We suggest that the results of Gruber and Compagno (1981), based on Holden's method (1974), may not be an accurate estimate; we believe ours to be more reasonable.

The size at maturity in different areas were similar, i.e. females matured at 332–341 cm TL in this area (Chen et al., 1997), 355 cm TL in the northwestern Atlantic (Stillwell and Casey, 1976), and 340 cm TL in the northeastern Atlantic (Moreno and Moron, 1992). Males matured at 270.1–287.9 cm TL in this area (Chen et al., 1997), 290–300 cm TL in the northwestern Atlantic (Stillwell and Casey, 1976), and 276 cm TL in the northeastern Atlantic (Moreno and Moron, 1992). Thus, size at maturity of the northwestern Pacific populations of *A. superciliosus* was very similar to those of populations elsewhere (Chen et al., 1997).

The maximum TL for female bigeye thresher sharks was 450 cm in Florida waters (Gilmore, 1983), 452 cm in Cuba (Guitart, 1975), 458 cm in New Zealand (Grey, 1928), and 422 cm and 357 cm, female and male, respectively, in this study. Possible reasons why this species is smaller in northeastern Taiwan than in other waters may be due to different environments, genes, gear selection, sampling bias, and fishing mortality.

Age and growth assessment of sharks from hard parts has been verified by length-frequency analysis to increase accuracy (Stevens, 1975; Pratt and Casey, 1983; Natanson et al., 1995). In this study, vertebral and

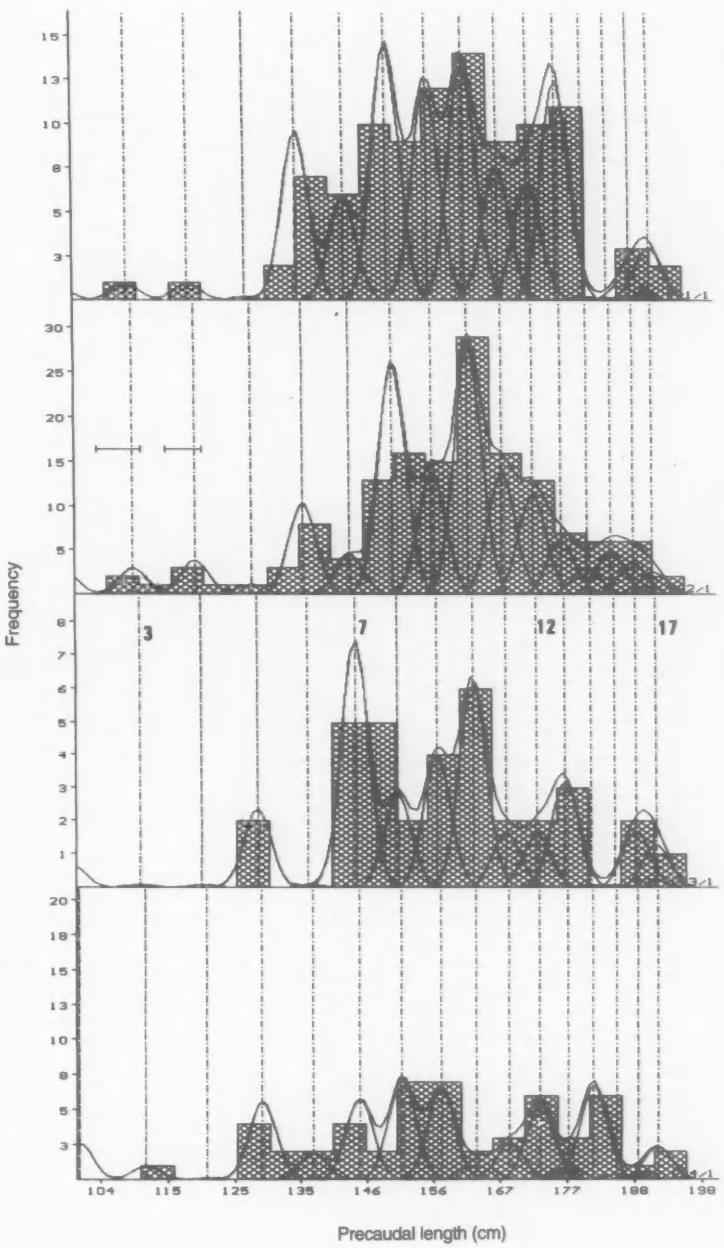

Figure 8

Length-frequency histograms for male *Alopias superciliosus* used in the analysis, and results of the best data fits. Horizontal bars indicate the constraints imposed to mean length at age.

length-frequency data were analyzed independently to derive estimates of the von Bertalanffy growth parameters for the bigeye thresher shark. Parameter estimation with MULTIFAN was based on the maximum likelihood method which has been successfully applied to various marine animals (Fournier et al., 1990; Haist and Porter, 1993; Bigelow et al., 1995; Pagavino and Gaertner, 1995). Growth curves derived from MULTIFAN and vertebral band counts are in good agreement for females but the former method yields larger size at age than the latter for males (Figs. 5 and 6). In addition, the similar values of VBGE parameters derived from MULTIFAN and vertebral band counts suggest that the age and growth estimation for bigeye thresher sharks in this study is reliable. The age classes (20 and 18) sliced by MULTIFAN from length-frequency data are less than those from vertebral reading (21 and 20). Small sample size and overlapping lengths at older ages may obscure length modes (Ernizi, 1990), and length-frequency estimates may be somewhat biased because of limitations of data and properties of length-frequency methods (Majkowski et al., 1987; Shepherd et al., 1987; Natanson and Cailliet, 1990). Thus, the vertebral method is considered more robust and the length-frequency analysis is used for verification only.

Acknowledgments

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Declines in nearshore rockfish recruitment and populations in the southern California Bight as measured by impingement rates in coastal electrical power generating stations

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Abstract.—We used data from fish-impingement studies of the coastal electric generating stations of Southern California Edison Company to examine patterns of nearshore rockfish abundance in the southern California Bight. The impingement data spanned 17 years (1977–93), comprised a minimum of several surveys per month and included power plants from throughout much of the Bight. Sixteen rockfish species were taken and six (olive rockfish, *Sebastes serranoides*; brown rockfish, *S. auriculatus*; bocaccio, *S. paucispinis*; blue rockfish, *S. mystinus*; treefish, *S. serriceps*; and grass rockfish, *S. rastrelliger*) accounted for 99% of all rockfish caught. Most of these fishes were between 0 and 2 years old. Catch rates for all six of these species have dropped substantially since the inception of the survey in 1977. Catch rates peaked in the early 1980s, dropped by a factor of over 100 to a low in 1984, and have generally remained low through 1993. One species, blue rockfish, has not been taken since 1984. We compared our rockfish impingement data from one power station in King Harbor, Redondo Beach, with data from scuba transects conducted during the same period within King Harbor. The results of the two surveys strongly suggest that the catch rates of rockfishes by power plants reflect the abundance of these fishes surrounding the plants. We suggest that the reduction in the abundance of nearshore rockfishes in the southern California Bight is due to both decreased recruitment success, reflecting long-term adverse oceanographic conditions, and to overfishing.

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The oceanographic regime off southern California is extremely dynamic, undergoing decadal changes in temperature, upwelling, and offshore transport (Roemmich and McGowan, 1995; MacCall, 1996). Beginning in 1976, the waters of the southern California Bight (SCB) began to warm and temperatures have generally remained warmer than those of the previous four decades (MacCall, 1996), characterizing part of a process of fluctuating water temperatures that has occurred for thousands of years (Soutar, 1967; Soutar and Isaacs, 1974; Baumgartner et al., 1992).

This warming trend is associated with a decline in upwelling and subsequent decreased zooplankton biomass (Roemmich and McGowan, 1995; Hayward et al., 1996). In addition, several studies in the SCB indicate that this change in the physical regime has led to changes in reef fish population size, community structure, and recruitment (Stephens et al., 1986; Holbrook and Schmitt, 1996). An ongoing 20-year survey at King Harbor, Redondo Beach, as well as one of 13 years duration at Santa Cruz Island, northern Channel Islands, has documented population declines in many fish species (Stephens et al., 1994; Holbrook and Schmitt, 1996). In particular, the King Harbor study shows a severe decline in the abundances of rockfishes (genus *Sebastes*). Some species, such as the blue rockfish, *S. mystinus*, that were very common in the mid-1970s, virtually disappeared by the mid-1980s and have remained absent (Stephens et al., 1986, 1994).

Despite widespread recognition that long-term data are essential for understanding population fluctuations and for correlating changes in population size with environmental events, most studies of reef fishes are limited in both temporal and spatial scales. The few cases where populations have been tracked for many years are limited in spatial scale. Both the Santa Cruz Island and the King Harbor studies, although of relatively long duration, have tracked fish populations at only a single site. A more accurate portrayal of fish abundances would come from multisite surveys, conducted over a number of years. Data from the fish-impingement studies

Figure 1

Location of the eight Southern California Edison coastal electric generating stations. For this survey, we used fish-impingement data from the four stations indicated in bold.

of the Southern California Edison Company (SCE) provide a unique long-term look at fish populations in the SCB. The impingement data are relatively long-term (17 years), are collected at fine temporal resolution (at minimum several surveys per month), and encompass much of the broad spatial distribution of the SCB.

This paper is the first in a series investigating changes in fish abundances over the past 17 years in the SCB using the extensive data set collected by SCE. Here, we report on patterns of rockfish (genus *Sebastes*) impingement from 1977 to 1993. Although rockfish made up slightly less than 1% of all species impinged in the SCE stations, as a group they are extremely important in both recreational and commercial fisheries in southern California (Wine[1]; Ally et al.[2]; Barsky[3]). In addition to documenting changes in abundance of common species, we discuss patterns of change in abundance in relation to changes in sea surface temperature over the same time period.

Materials and methods

Data on fish impingement were obtained from the biological monitoring program conducted by Southern California Edison at coastal electric generating stations throughout much of the SCB. Although fish impingement was monitored at all eight stations, we chose to analyze data from the four stations that had the most continuous sampling effort over the period 1977–93 (Fig. 1). Three of the plants, Ormond Beach, Redondo Beach, and Huntington Beach, are fossil fuel fired; San Onofre is a nuclear generating station. Although the timing of sampling among the stations was haphazard, samples were taken at least once and up to 11 days per month. The number of samples taken per year at each station are shown in Table 1.

All power plant intakes are situated on sandy bottom and all are surrounded by varying amounts of rock rubble. Intake openings are at approximately equal depths (8–10 m) with the exception of Redondo Beach station where intakes are situated in slightly deeper water (14 m). The intake openings vary in their distance to the shoreline from 285 m at Redondo Beach to 965 m at San Onofre.

[1] Wine, V. 1979. Southern California independent sport fishing survey. Annual report. 3. Calif. Dep. Fish Game, Mar. Res., Admin. Rep. 79-3.

[2] Ally, J. R. R., D. S. Ono, R. B. Read, and M. Wallace. 1991. Status of major southern California marine sport fish species with management , based on analyses of catch and size composition data collected on board commercial passenger fishing vessels from 1985 through 1987. Calif. Dep. Fish and Game, Mar. Res. Div., Admin. Rep. 90-2, 376 p.

[3] Barsky, K. 1996. California Department of Fish and Game, 530 E. Montecito St., Santa Barbara, CA, 93103. Personal commun.

Table 1

Number of fish-impingement samples taken during normal operations at four coastal electrical power generating stations from 1977 to 93.

Year	Huntington Beach	Ormond	Redondo (units 7–8)	San Onofre 1	San Onofre 2	San Onofre 3
1977	0	0	87	76	0	0
1978	13	13	67	90	0	0
1979	55	68	73	93	0	0
1980	98	100	103	34	0	0
1981	60	58	52	42	0	0
1982	47	43	35	19	27	0
1983	57	55	48	23	61	8
1984	57	50	58	28	65	70
1985	56	54	55	63	84	67
1986	53	57	49	28	69	101
1987	45	57	43	51	57	60
1988	41	47	25	42	57	47
1989	38	46	47	40	46	58
1990	26	37	30	36	55	43
1991	16	43	50	48	46	57
1992	37	44	38	58	78	68
1993	67	40	31	24	65	69
Total	753	799	737	629	710	648

All data presented were obtained during "normal" power plant operations. During normal operation, fishes are entrained in the cooling water and flow through conduits to the station where they are impinged on traveling screens in the forebay of the power plant. "Normal" fish-impingement surveys consist of counting all fishes impinged during a 24-h period of routine plant operations (e.g. on full flow days). Impinged fishes are separated from incidental debris, sorted by species, identified, counted, and measured to standard length (mm).

Because flow rates differed slightly among stations and years, all abundance data are presented as the number of fishes per million gallons of water passing through the intake. Flow rates also varied within each station from month to month but remained constant during any given month. Thus, it was necessary to calculate monthly mean catch rates for each site. Annual mean catch rates are presented in this paper. For most analyses, annual catch is the grand mean of all monthly means across all sites for that year. For one comparison, mean annual catch rates are calculated for the Redondo station only.

Table 2

Number of rockfish impinged during normal operations at four coastal electrical power generating stations from 1977 to 93.

Species	Common name	Number
Sebastes serranoides	Olive rockfish	14,571
S. auriculatus	Brown rockfish	5586
S. paucispinis	Bocaccio	3262
S. mystinus	Blue rockfish	1640
S. serriceps	Treefish	1124
S. rastrelliger	Grass rockfish	1092
Sebastes spp.	Unidentified rockfish	129
S. carnatus	Gopher rockfish	65
S. dalli	Calico rockfish	44
S. caurinus	Copper rockfish	9
S. miniatus	Vermilion rockfish	8
S. atrovirens	Kelp rockfish	8
S. goodei	Chilipepper	5
S. melanops	Black rockfish	2
S. ovalis	Speckled rockfish	1
S. maliger	Quillback rockfish	1
S. flavidus	Yellowtail rockfish	1
	Total rockfish	27,546

Results

During this survey, 27,546 rockfishes, representing 16 identifiable species, were caught (Table 2). Olive rockfish (*Sebastes serranoides*) were the most commonly taken, followed by brown rockfish (*S. auriculatus*), bocaccio (*S. paucispinis*), blue rockfish (*S. mystinus*), treefish (*S. serriceps*), and grass rockfish (*S. rastrelliger*). These six most abundant species represented 99% of all rockfish caught. From the lengths of the fishes sampled (Fig. 2), we determined

that most of the rockfishes impinged were between 0 and 2 years old (Love and Westphal, 1981; Love et al., 1990; Love and Johnson, in press).

The life histories of these six species encompass a range of habitat preferences and behaviors. Olive rockfish and blue rockfish are nearshore, midwater fishes. Grass rockfish and treefish are shallow-water benthic species, usually inhabiting high relief. Brown rockfish are found primarily along sand-rock interfaces or over low relief. Bocaccio are midwater fish; the young are found in shallow water and they migrate into deeper water as subadults (Feder et al., 1974).

We analyzed abundance patterns over time for all rockfishes combined and separately for the six most common species. Since the inception of the survey in 1977, mean catch rates for all rockfishes combined have dropped substantially (Fig. 3). Catch rates peaked in the early 1980s, dropped precipitously (by a factor of over 100) to a low in 1984 and have generally remained low through 1993. The exception was a one-year, nearly tenfold rise between 1987 and 1988 which was due primarily to a large influx of young bocaccio, although olive, brown, and grass rockfish catches also increased slightly during this period (Fig. 4).

Despite very different life histories, the six most abundant species showed generally similar impingement patterns over time (Fig. 4). In all six species, peak impingement occurred in the late 1970s or early 1980s. Maximum catches occurred in 1977 (bocaccio), 1980 (grass, blue, and brown rockfish), or 1981 (olive rockfish and treefish). Between 1983 and 1993, with only one exception, impingement of these six species was either extremely low or nonexistent. The exception occurred in 1988, when relatively large numbers of bocaccio were impinged. The 1988 peak in bocaccio abundance was the result of catches at only two stations, Redondo and San Onofre, in May of that year.

Between the late 1970s and early 1990s, there was a sharp drop in the amount of rockfish impingement in the SCE coastal generating stations. We believe that this pattern reflects the abundance of these fishes in nearshore waters at the time. To address this issue, we compared our impingement data for olive rockfish, blue rockfish, and bocaccio with that from visual diving surveys conducted on transects in King Harbor, Redondo Beach (Stephens[4]). The visual surveys primarily record juvenile abundance

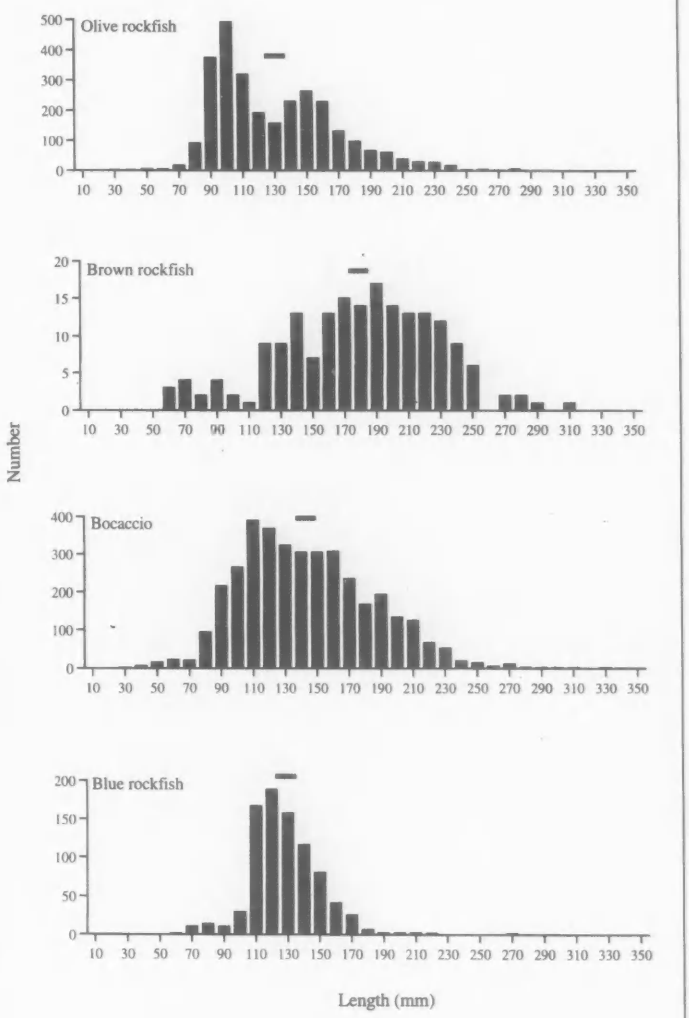

Figure 2

Length frequencies (standard length mm) of the four most commonly observed rockfishes in the Southern California Edison impingement studies, 1977–93. Short lines above bars indicate mean length.

[4] Stephens, J. 1997. Department of Biology, Occidental College, 1600 Campus Rd., Los Angeles, CA, 90041. Unpubl. data.

because rockfish of the three target species tend not to remain in King Harbor as adults. For this comparison, we used only the yearly catch rates from the Redondo Beach electrical power generating station that is closest to the King Harbor transects. In the dive survey, all three species were common during the mid- to late-1970s (Fig. 5). However, by 1980, individuals of these species were rarely seen. Blue rockfish and bocaccio have not been observed since that time. Olive rockfish have remained scarce, although small population increases were noted in the late 1980s and early 1990s. The patterns of impingement for these three species at Redondo show similar trends to that from the diver surveys. During the late 1970s, olive rockfish were commonly impinged but catches declined markedly by 1980 (Fig. 5). Two of the slight increases noted in the diver survey in 1985 and 1991 were reflected in the impingement study, although the magnitude of the increase is greater in the SCE data in 1985 and in the diver surveys in 1991. In the impingement survey, blue rockfish catches were relatively high in the late 1970s and declined to zero in 1981 (Fig. 5). This pattern matches precisely the pattern observed in the diver surveys, with one exception. The exception was a one-day pulse of small blue rockfish caught in a single day at the Redondo station in 1982. Regarding blue rockfish, the two data sets are in general agreement; no blue rockfish have either been observed or captured since 1983. Changes in abundance of bocaccio are also similar between the impingement data and the diver surveys (Fig. 5), with the exception of a large pulse of young bocaccio impinged during a single collection in 1988.

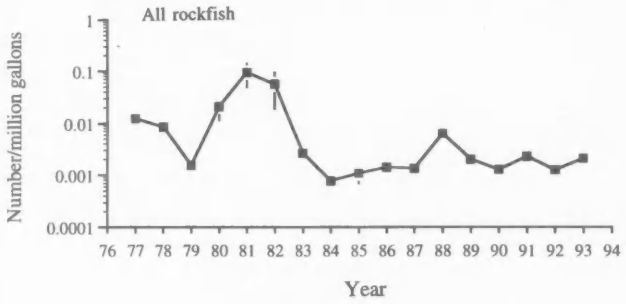

Figure 3

Annual number of rockfishes impinged per million gallons of water pumped, for all species of rockfishes combined, 1977–93. Note log scale. See text for description of the calculation of mean. Error bars are ±1 SE.

Discussion

From at least the 1950s through the late 1970s, black-and-yellow, blue, gopher, and olive rockfishes, as well as young bocaccio, were important components of the inshore rocky reef community of the SCB (Limbaugh, 1955; Ebeling et al., 1980; Larson, 1980; Stephens et al., 1984, 1986; Patton et al., 1985). In particular, blue rockfish and olive rockfish were among the dominant species over many reefs (Carlisle et al., 1964, Ebeling et al., 1980). However, since the early 1980s, most species of rockfishes have nearly disappeared from the nearshore waters of the SCB (Stephens et al., 1994; Larson[5]; Schroeder[6]). On many of the reefs that once held substantial numbers of these species, very few rockfishes remain. Results of the fish-impingement surveys conducted since 1977 support the observation that several species of rockfish are less abundant now than in the late 70s and early 80s. We find it particularly compelling that for at least two species (blue rockfish and grass rockfish), not a single individual was collected in the past ten (blue rockfish) or three (grass rockfish) years.

We feel that the pattern of changing abundance in the impingement study is an accurate reflection of the pattern of change in the nearshore environment. Despite two very different survey methods, the patterns of rockfish abundance derived from the impingement data and the visual survey data from King Harbor were similar. On the gross level, the patterns for three species show amazing similarity; all have declined drastically since the late 70s and have remained low in the 80s and early 90s. On a finer scale, there were several large peaks in the impingement data that were not evident in the visual survey data (Fig. 5: blue rockfish in 1982, bocaccio in 1988). These differences may be due to differences in the ages of some of the fish recorded in the two surveys. Although the visual surveys mainly record juvenile blue rockfish, olive rockfish, and bocaccio, they may occasionally include older individuals, whose population levels may be buffered from the potentially large variations in recruitment by mortality. The impingement collections comprised mainly 0–2 year olds. Both of the large pulses seen in the impingement data were collections taken on a single day.

[5] Larson, R. 1997. Department of Biological Sciences, San Francisco State University, San Francisco, CA 94132. Personal commun.

[6] Schroeder, D. 1997. Marine Science Institute, University of California, Santa Barbara, CA 93106. Personal commun.

It is likely that the decline in rockfish abundance in the southern California Bight was well underway by 1977 when the current impingement surveys started. The King Harbor survey began in 1974 and results showed that the abundance of blue rockfish and bocaccio were at much higher levels from 1974 to 1977 than in later years. For example, blue rockfish were extremely abundant in King Harbor in 1974 but since 1983, not a single blue rockfish has been observed or impinged. There were also occasional impingement collections dating back to 1975 and these also indicate that pre-1977 rockfish catches were as high or higher than 1977 levels. These pre-1977 impingement surveys were too temporally sparse to be included in the complete data set, but they are suggestive. Thus, it appears that, despite larger variation in year to year rockfish impingement during the late 70s and early 80s, there has been an overall decrease since that time which probably reflects a decrease in nearshore populations of these species throughout the southern California Bight (Stephens[4]; Love et al., in press).

Although none of the previously mentioned nearshore studies conducted during the 1950s–1970s were designed to focus on rockfish year-class strength, it appears from these surveys that the widespread abundance of nearshore rockfishes before the early 1980s was generated by a series of strong year classes. During this same period, Southern California trawl studies of two other deeper-dwelling rockfish species implied a similar phenomenon (Mearns et al., 1980). It is likely that recent declines in abundance of these nearshore species were due to a decade-long series of very poor year classes.

What might be responsible for this poor rockfish recruitment? The succession of poor year classes off southern California is likely linked to decade-long changes in oceanographic conditions. Most rockfishes are primatively viviparous (Boehlert et al., 1987) and rockfish larvae are found primarily in the upper mixed layer (Ralston and Howard, 1995). After approximately one month, rockfish larvae metamorphose into pelagic juveniles that spend 3–6 months in the water column as plankton and micronekton

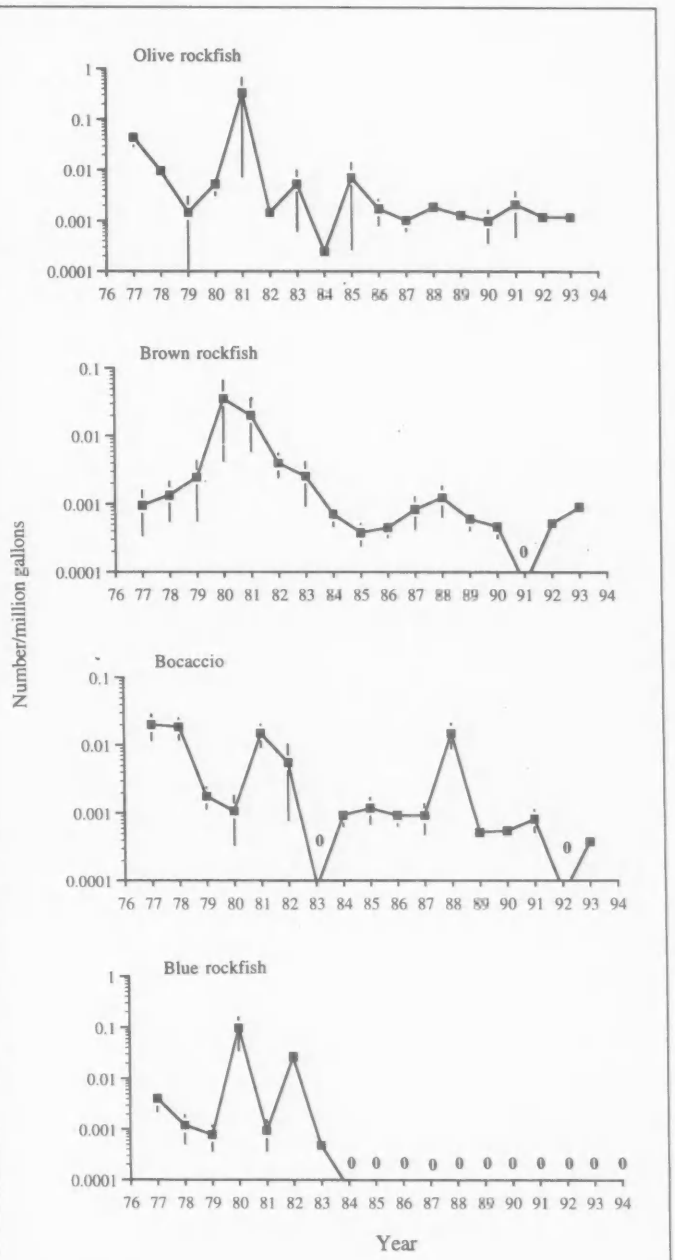
Olive rockfish
Brown rockfish
Bocaccio
Blue rockfish
Number/million gallons
Year
76 77 78 79 80 81 82 83 84 85 86 87 88 89 90 91 92 93 94

Figure 4

Annual number of rockfishes impinged per million gallons of water pumped for the six most commonly impinged species, 1977–93. Note log scale. See text for description of the calculation of mean. Error bars are ±1 SE.

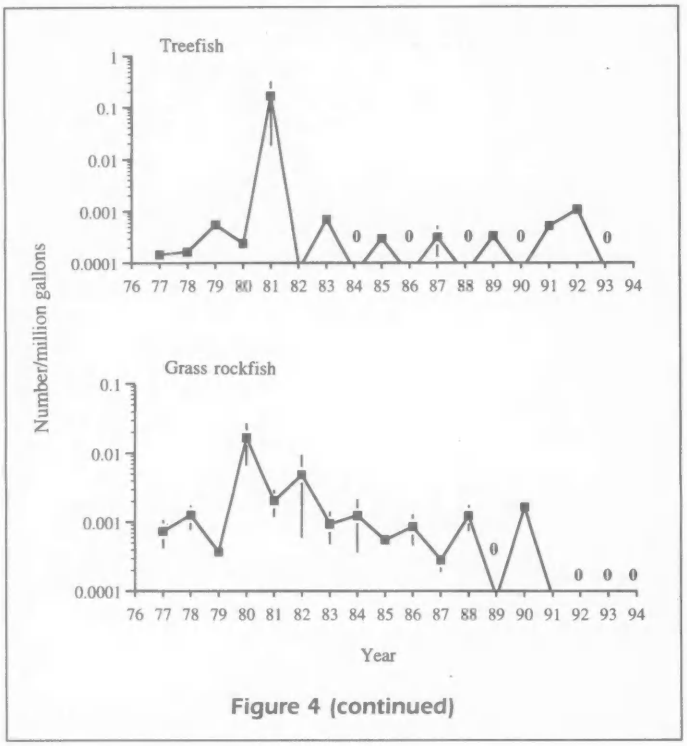

Figure 4 (continued)

(Love et al., 1991). It is during the larval and pelagic juvenile stages that rockfish year-class strength is determined (Ralston and Howard, 1995) and upwelling appears to be a particularly important factor affecting survival during these stages. Years with intermediate levels of upwelling seem to correspond with strong year classes (Ainley et al., 1993).

Since the late 1970s, waters in the southern California Bight have warmed approximately 1.5°C and upwelling has declined to approximately one half of the levels observed in the late 70s and early 80s (Norton and Crooke, 1994). In turn, this has led to reduced zooplankton production (Roemmich and McGowan, 1995) and an apparent reduction in the larval and juvenile survivorship of many marine fish species (Holbrook and Schmitt, 1996). The current low-upwelling conditions are probably part of a long-term alternation of warm- and cold-water regimes that extend along much of the northeast Pacific (MacCall, 1996). Poor pelagic juvenile rockfish survivorship of many species also extends at least into central and northern California (Ralston[7]). Juvenile bocaccio recruitment indices for central-northern California (Ralston et al., 1996) show a steady decline similar to the decline we observed for bocaccio in the impingement data.

There has also been a sharp decline in the numbers of both subadult and adult inshore rockfishes in southern California. These reductions are due both to natural mortality and heavy fishery exploitation. Unlike many deeper-water and more northerly species, the inshore rockfishes of California have relatively short life spans, often less than perhaps 25 years (Miller and Geibel, 1973; Love and Westphal, 1981; Love and Johnson, in press). Thus, even without fishing pressure, the number of adults of many of these species would tend to decrease relatively rapidly during extended periods of poor reproduction. In addition, these are also very heavily fished species. Until the early 1990s, most of the catch was made by recreational fishermen (Wine[1]; Ally et al.[2]). Beginning in the early 1990s, a live-fish commercial fishery developed that targets shallow-water species (Barsky[3]).

The sharp decreases in inshore rockfish populations are also mirrored by similar declines in the populations of deeper-water species. Between 1980 and 1996, it appears that there was also a substantial decrease in the numbers of deeper-water rockfishes off southern California. An analysis of the recreational rockfish catch in southern California since 1980 shows steep declines in catches of most of the important species (Love et al., in press). As an example, catches of chilipepper rockfish (*S. goodei*) have declined to 0.5%, bocaccio to 1%, and widow rockfish (*S. entomelas*) to 1.25% of 1980 levels. These declines are almost certainly reflective of lowered abundances of many species rather than a shift in fishing emphasis by recreational vessels.

It is generally held that although reef fish populations exhibit large temporal variations, even undergoing local extinctions, external sources of new young will eventually provide new recruits. Referring specifically to the California coast, MacCall (1996) speculated on the establishment of southern marine species, such as the Pacific seahorse (*Hippocampus ingens*), at the northern ends of their ranges off California. He noted that these animals probably establish themselves during warm-water periods and, in the absence of fishing pressure, may survive colder

[7] Ralston, S. 1996. National Marine Fisheries Service, Tiburon Laboratory, 3150 Paradise Dr., Tiburon, CA, 94920. Personal commun.

periods if the adults suffer low mortality. A similar phenomenon has been described for California sheephead (*Semicossyphus pulcher*) which exhibit episodic recruitment related to anomalous events in current flow (Cowen, 1985).

The reverse of this phenomena has occurred for at least some of the inshore rockfish species, particularly blue rockfish and olive rockfish. In the SCB, both species are near the southern end of their usual geographic ranges and large-scale recruitment may occur only during cold-water cycles, as occurred during the 1960s and early 1970s. During this current warm-water period, recruitment waned and the adult population was expected to decline slowly. However, the continuing fishing pressure on the populations accelerated this process.

On the basis of current flow in the SCB, it is likely that even during periods of successful recruitment, many of the rockfishes in southern California are generated from southern California adults (Reid et al., 1958; Schwartzlose, 1963; Browne, 1993). If true, the sharp drop in the adult populations of many rockfishes is particularly troubling and raises the issue of recruitment overfishing. This is a particularly strong possibility because there is little incentive for recreational anglers to decrease fishing activities on shallow reefs. These rockfishes are caught as part of a species assemblage that includes not only various rockfishes, but also such species as kelp bass (*Paralabrax clathratus*), Pacific barracuda (*Sphyraena argentea*), California sheephead (*Semicossyphus pulcher*), and ocean whitefish (*Caulolatilus princeps*). As long as even moderate numbers of any recreational reef species are taken, recreational vessels will continue to fish on rockfish-depleted reefs and continue to reduce already low numbers of rockfish. Because virtually all inshore reefs in southern California are heavily fished, successful recruitment will likely continute to be hazardous.

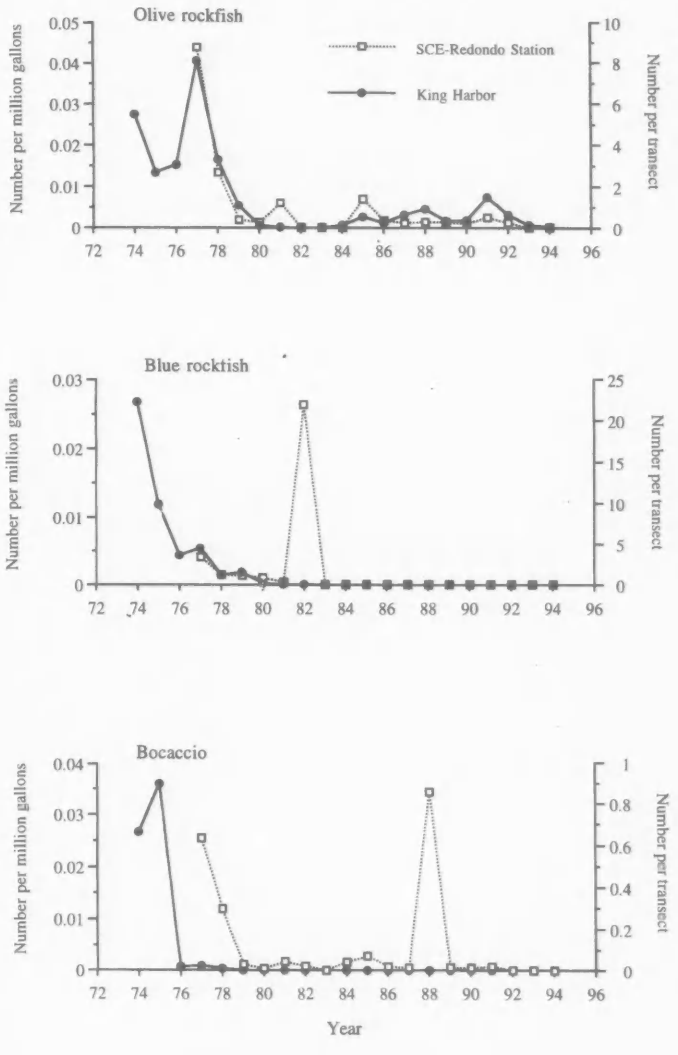

Figure 5

A comparison of impingement and diver observations of olive rockfish, blue rockfish and bocaccio from King Harbor, Redondo Beach (1974–94, Stephens[4]) and the SCE Redondo Beach station (1977–94, this study).

Acknowledgments

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Geographic variation in genetic and growth patterns of Atka mackerel, *Pleurogrammus monopterygius* (Hexagrammidae), in the Aleutian archipelago

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Abstract.—Atka mackerel, *Pleurogrammus monopterygius*, growth data differed significantly by area for length and weight characteristics, suggesting that local aggregations of this species develop differential growth patterns. We analyzed length-at-age and weight-length growth patterns from over 500 fish and 37 protein-coding gene loci to determine the relation among Atka mackerel stocks in the Aleutian Islands. However, the potential stock delineations based on the growth patterns were not supported by the genetic data. Atka mackerel showed a high degree of genetic variability. Variation was detected at 30 of 37 loci; 14 of the 30 loci were variable at the $P_{0.95}$ level. Average heterozygosity for 329 specimens was 0.137, an unusually high value for a marine fish. Between-sample variation among samples was extremely low (F_{ST}=0.004), suggesting considerable gene flow throughout the range represented by the samples. On the basis of the genetic data, we cannot reject the null hypothesis that our samples came from a single genetically homogenous population of Atka mackerel. We presume that gene flow occurs throughout the population through the dispersal of pelagic larvae and juveniles. We conclude that despite genetic homogenization, phenotypic variation in Atka mackerel adult life history stages warrants consideration by fishery managers.

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Fishery Bulletin 96:502–515 (1998).

Atka mackerel, *Pleurogrammus monopterygius*, a member of the greenling family Hexagrammidae, is distributed throughout the north Pacific Ocean, the southern Bering Sea, and the Gulf of Alaska. The center of abundance of this semipelagic species is the Aleutian Islands.[1] Greenling larvae and fingerlings (25–30 mm) undergo a pelagic stage and assume an oceanic mode, during which time they reside in the surface layers of the open waters and migrate for considerable distances out to sea (Gorbunova, 1962). Adult (3+ years) Atka mackerel are pelagic during much of the year (in waters <200 m depth) but migrate annually to moderately shallow waters where they become demersal and spawn in areas of strong currents (Gorbunova, 1962). They have specific spawning site preferences and spawning has been observed in island passes in the Aleutian, Shumagin, and Commander Island archipelagoes (Turner, 1886; Rutenberg, 1962).

Historically, large inshore concentrations of spawning Atka mackerel have been the target of subsistence fisheries by native Aleuts (Turner, 1886). The first large-scale commercial catches in the Aleutian Islands and western Gulf of Alaska were taken by Russian fleets beginning in the early 1970s, followed by the Republic of Korea, and to a lesser extent, Japan in the early 1980s (Murai et al., 1981; Berger et al., 1986). Presently, a U.S. trawl fishery harvests Atka mackerel from the eastern Bering Sea and Aleutian Islands regions, with minimal catches from the Gulf of Alaska. From 1992 to 1994, catches averaged about 70,000 metric tons (t) (valued at 17 million U.S. dollars [exvessel] in 1994) and increased to 104,000 t in 1996.[1,2]

[1] Lowe, S. A., and L. W. Fritz. 1996a. Atka mackerel. *In* Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions as projected for 1997, p. 369–420. North Pacific Fishery Management Council, 605 W. 4th Avenue, Suite 306, Anchorage, AK 99501-2252.

[2] Lowe, S. A., and L. W. Fritz. 1996. Atka mackerel. *In* Stock Assessment and Fishery Evaluation Report for the Groundfish Resources of the Gulf of Alaska as projected for 1997, p. 331–361. North Pacific Fisheries Management Council, 605 W. 4th Avenue, Suite, Anchorage, AK 99501-2252.

An analysis of morphological and meristic data by a Russian scientist indicated separate populations in the Gulf of Alaska and the Aleutian Islands.[3] The meristic study compared the number of dorsal, anal, and pectoral fin rays, total number of vertebrae, and number of gill rakers on the first gill arch from a sample of 100 fish collected off Kodiak Island in the Gulf of Alaska and the Rat Islands in the Aleutian Islands. The morphological study consisted of a statistical comparison of various partial fish body lengths as a percentage of fork length, by area. Lee (1985) also conducted a morphological study analyzing the covariance between four partial fish lengths and fork length by area and sex from samples taken from the Bering Sea, Aleutian Islands, and the Gulf of Alaska. The data showed some differences (although not consistent by area for each characteristic), suggesting a certain degree of reproductive isolation. On the basis of an analysis of variance of Aleutian Islands growth data with year, area, and sex as factors, Kimura and Ronholt (1988) found significant differences in weight and length-at-age of Atka mackerel from six different areas in the Aleutian Islands, indicating potential stock differentiation. Kimura and Ronholt (1988) suggested therefore that Atka mackerel appear to be distributed in localized groups or assemblages once they assume the more demersal phase of their life history. Recent analysis of Aleutian Islands Atka mackerel growth data by current fishery management areas shows a distinctive size cline, with length at age smallest in the western Aleutians and largest in the eastern Aleutians[1,2]

Differential growth by area can be an indication of stock delineations. The presumption for Atka mackerel, based on the morphological and growth analyses, was of at least a discontinuous distribution throughout the Aleutian Archipelago. Genetic tests are necessary to confirm separate stocks and help to further our understanding of the life history and distribution patterns of Atka mackerel. Information about the extent and nature of stock differences is also critical to improve stock assessments for long-term management of the Atka mackerel fisheries in the Gulf of Alaska and Aleutian Islands. To date, there have been no population genetics surveys of this species to determine the existence of discrete stocks.

A preliminary survey of allozymes from 40 individuals indicated a sufficient number of polymorphic loci to conduct a full study of the genetic population structure of this species (Winans et al., 1995). We report here 1) length-at-age and length-weight relations derived from samples taken throughout the Aleutian Archipelago and 2) a genetic survey of Atka mackerel from samples taken from four locations in the Aleutian Islands ranging from 169°W to 172°E (Fig. 1). Our null hypothesis is that there are no differences between samples taken along the Aleutian Archipelago, from Umnak Island in the east to Attu Island in the west.

Materials and methods

Age, weight, and length data

Biological samples and length and weight information were collected during National Marine Fisheries Service (NMFS) triennial trawl surveys, June to August of 1993 and 1994, from the Gulf of Alaska and Aleutian Islands region, respectively. The sampling coincided with the summer spawning period of Atka mackerel (July to October; McDermott and Lowe, 1997). Random samples of Atka mackerel from the trawl survey catches were sorted by sex, and individual weight and fork-length data were collected. Length was estimated to the nearest one centimeter, and weight was estimated to the nearest gram with a platform scale when weather conditions allowed (Martin and Clausen, 1995). Age structures (sagittal otoliths) were collected by using a length-stratified sampling scheme of five fish per sex, per centimeter length category. An attempt was made to distribute the otolith collections over the entire survey area. Otoliths were placed in vials with 50% ethanol, and age was determined by personnel in the NMFS Age Determination Laboratory.

A total of 510 otoliths were collected and aged (Table 1). Otoliths were prepared by snapping each along the dorsal-ventral plane and passing the broken surface over a flame. The burnt cross-section was examined under a dissecting microscope and illuminated by reflected light (Anderl et. al, 1996).

Growth parameters were estimated by fitting the age-length data to the widely used von Bertalanffy (1938) growth equation:

$$l_t = L_\infty\left(1-e^{-K(t-t_0)}\right),$$

which expresses length at age t (l_t) as a function of three parameters: L_∞, K, and t_0. As age increases, length approaches L_∞, which is the mean asymptotic length. The slope of the von Bertalanffy curve continuously decreases with increasing age as l_t approaches the asymptotic length. This rate of decrease is described by K. The parameter t_0 is the theoretical time a fish would have been zero length. The

[3] Levada, T. P. 1979. Comparative morphological study of Atka mackerel. Pac. Sci. Res. Inst. Fish. Oceanogr. 5(TINRO), Vladivostok, U.S.S.R. Unpubl. manuscript, 7 p.

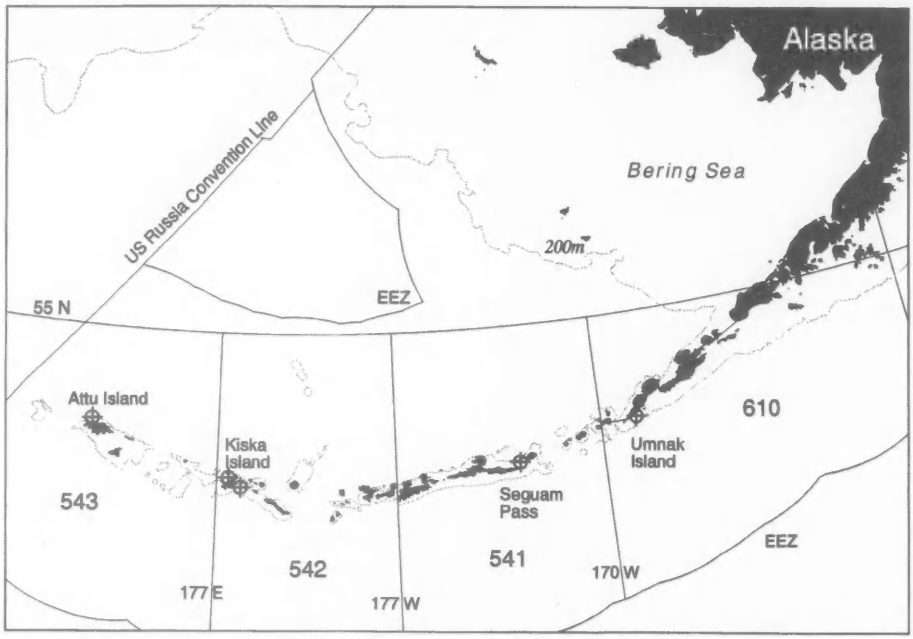

Figure 1

Locations of Atka mackerel sample collections in the western Aleutian (543), central Aleutian (542), and eastern Aleutian Islands (541), and western Gulf of Alaska (610) fishery management areas. The U.S. Exclusive Economic Zone (EEZ) is also shown.

growth parameters were determined with a nonlinear least squares procedure (FISHPARM[4]).

Similarly, length-weight relationships were estimated from the following equation:

$$w = al^b,$$

where weight (w) varies as a power (b) of length (l). The coefficients a and b were estimated for each of the four management areas with a nonlinear least squares procedure (FISHPARM[4]). On the basis of the work of Kimura and Ronholt (1988), who found that sex was not an important differentiating variable for growth in Atka mackerel, we present growth curves for the sexes combined.

The age-length and length-weight growth curves for the four management areas were estimated and compared with an F-test. To further test for the significance of the differences among areas, regardless of the fit to the von Bertalanffy or length-weight curves, a two-factor analysis of variance (ANOVA) was applied to the age-length and the length-weight data with SPLUS software (Chambers and Hastie, 1992). The age-length ANOVA included age and area as factors and an age × area interaction term, and

Table 1

Sample sizes of aged Atka mackerel otoliths from the Gulf of Alaska (area 610), eastern Aleutian Islands (area 541), central Aleutian Islands (area 542), and western Aleutian Islands (area 543) fishery management areas (Fig. 1).

Age (yr)	Gulf of Alaska (610)	Eastern Aleutian Islands (541)	Central Aleutian Islands (542)	Western Aleutian Islands (543)	Total
2	22	2	18	19	61
3	1	7	55	53	116
4	19	9	22	10	60
5	43	15	30	25	113
6	9	44	19	20	92
7	1	8	7	5	21
8	0	7	7	8	22
9	0	1	4	5	10
10	0	1	1	13	15
Total	95	94	163	158	510

[4] Prager, M. H., C. W. Recksiek, and S. B. Saila. 1987. Nonlinear parameter estimation for fisheries. Michael Prager, Old Dominion University, Dep. of Oceanography, Norfolk, VA 23508. Unpubl. documentation.

Table 2

Enzymes examined for allozyme variation. Enzyme commission (EC) numbers follow the IUBMBNC (1992). Tissues examined were muscle (M) and liver (L). Buffers used are described by Aebersold et al. (1987) except for the ACEN7 gel, which is an ACE7 gel with 0.015% beta-nicotinamide adenine dinucleotide added to the gel and which has cathodal electrode buffers.

Enzyme name	EC Number	Locus	Tissue	Buffer
Beta-*N*-Acetylgalactosaminidase	3.2.1.53	*bGALA**	L	ACE7
N-Acetyl-beta-glucosaminidase	3.2.1.30	*bGLUA**	L	ACE7
Aconitate hydratase	4.2.1.3	*AH-1**	M	ACE7
		*AH-2**	L	ACE7
Adenosine deaminase	3.5.4.4	*ADA**	M	TBE
Adenylate kinase	2.7.4.3	*AK**	M	ACE7
Alanine aminotransferase	2.6.1.2	*ALAT**	M	TBE
Alcohol dehydrogenase	1.1.1.1	*ADH**	L	ACE7
Aspartate aminotransferase	2.6.1.1	*AAT-1**	M	ACE7
		*AAT-2**	L	TBCLE, TBE
		*AAT-3**	M	TBCLE, TBE
Creatine kinase	2.7.3.2	*CK**	M	TBCLE
Esterase	3.1.1.-	*EST**	M	TBCLE
Enolase	4.2.1.11	*ENO**	M	ACE7
Fumarate hydratase	4.2.1.2	*FH**	M	ACEN7
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-1**	M	TBCLE
		*GPI-2**	M	TBCLE
Glycerol-3-phosphate dehydrogenase (NAD$^+$)	1.1.1.8	*G3PDH-1**	M	ACEN7
		*G3PDH-2**	M	ACEN7
L-Iditol dehydrogenase	1.1.1.14	*IDDH**	L	TBCL
Isocitrate dehydrogenase (NADP$^+$)	1.1.1.42	*IDHP-1**	L	ACE7
		*IDHP-2**	M	ACE7
L-Lactate dehydrogenase	1.1.1.27	*LDH**	M	ACE7
Malate dehydrogenase	1.1.1.37	*mMDH**	M	ACEN7
		*sMDH-1**	ML	ACEN7
		*sMDH-2**	M	ACEN7
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	M	TBE
Peptidase-C	3.4.-.-	*PEP-C**	M	TBE
Phosphoglucomutase	5.4.2.2	*PGM**	M	TBCLE, ACE7
Phosphogluconate dehydrogenase (decarboxylating)	1.1.1.44	*PGDH**	M	ACE7
Phosphoglycerate kinase	2.7.2.3	*PGK**	M	ACE7
Proline dipeptidase	3.4.13.9	*PEPD**	M	TBE
Pyruvate kinase	2.7.1.40	*PK**	M	ACE7
Superoxide dismutase	1.15.1.1	*SOD**	L	ACE7
Triose-phosphate isomerase	5.3.1.1	*TPI**	M	TBE
Tripeptide aminopeptidase	3.4.11.4	*PEPB-1**	M	TBE, TC4
		*PEPB-2**	M	TBE

the length-weight ANOVA included length and area factors and a length × area interaction term.

Genetic data

Genetic samples were collected from four locations throughout the Aleutian Archipelago (Fig. 1). Sample sizes were as follows: Attu Island, n=74; Kiska Island, n=80; Seguam Pass, n=100; and Umnak Island, n=75. Muscle and liver tissues were collected from each specimen for protein electrophoresis and placed in the onboard freezers until they could be transferred to a freezer set at –80°C.

Genetic variability was examined by using starch gel electrophoresis as described by Aebersold et al. (1987). Initially, we examined 36 enzyme systems, of which 28 were clearly resolved. Those 28 enzyme systems revealed 37 loci. Tissue and buffer combinations for each enzyme are listed in Table 2. Nomenclature for loci and alleles followed Shaklee et al. (1990).

Genetic variability within samples was estimated as average heterozygosity (mean proportion of heterozygous loci per individual), the percentage of polymorphic loci per sample at the $P_{0.95}$ level (frequency of the common allele ≤0.95), and the average num-

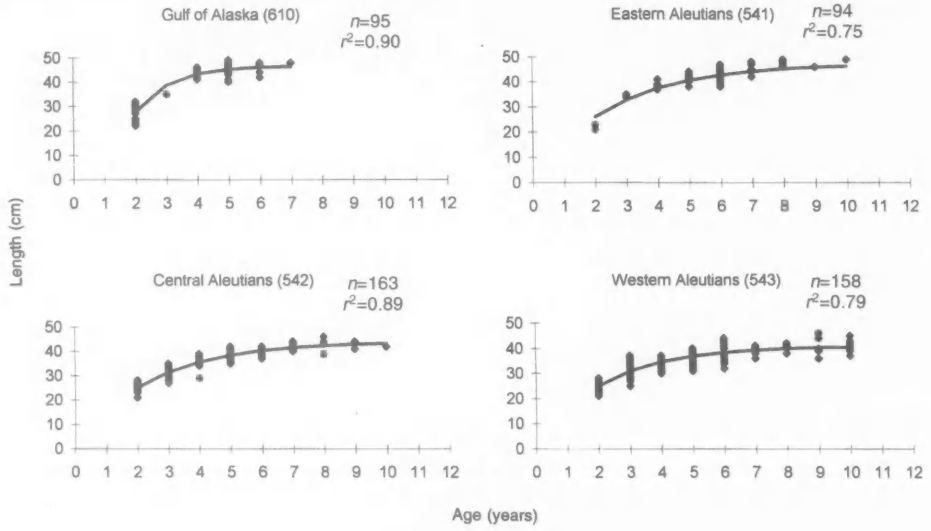

Figure 2

Atka mackerel age-length data by fishery management areas, collected from resource assessment surveys of the Gulf of Alaska and Aleutian Islands in 1993 and 1994, respectively. The fitted von Bertalanffy growth curves are plotted. Sample sizes (n) and the coefficients of determination (r^2) are given.

ber of alleles per locus. Samples were tested individually with chi-square analyses for conformance to expected Hardy-Weinberg proportions and as one pooled sample. The latter method tests the assumption that the samples are not different (i.e. represent one interbreeding population). Differences among samples were examined with Wright's fixation index F_{ST} and Nei's unbiased genetic distance statistic (Nei, 1978) and with standard chi-square contingency table analysis for the $P_{0.95}$ loci. Values of F_{ST} range from zero, indicating no population differentiation, to one, indicating fixation for alternate alleles. Genetic analyses were conducted using the BIOSYS-1 computer program (Swofford and Selander, 1981).

Results

Age, weight, and length data

Sample sizes were relatively small when stratified by area, ranging from 95 to 163. Sampled fish lengths ranged from 21 to 49 cm, ages from 2 to 10 years, and weights from 0.084 to 1.9 kg (Figs. 2 and 3). The relatively high coefficients of determination (r^2) indicated good fits to the von Bertalanffy and length-weight models (Figs. 2 and 3). An examination of the residuals also indicated no obvious patterns, and the variances of the residuals were homogeneous by age and area for the von Bertalanffy model, and by length and area for the length-weight model. The fitted growth curves for each management are shown together in Figures 4 and 5; Table 3 gives the estimated parameters and standard errors. The F-tests revealed that differences in the growth curves among areas were significant ($P<0.0005$) for both the age-length and length-weight data. Because of the low sample sizes for the Gulf of Alaska and eastern Aleutian Islands data, and low numbers of fish in the Gulf of Alaska greater than five years, these data were combined and fit to the von Bertalanffy model. An F-test to test for differences between these two specific data sets was highly significant ($P<0.0005$).

The results of the two-way factorial analysis of age-length and length-weight data were highly significant (P of $F \leq 0.0001$, Tables 4 and 5). To account for unequal sample sizes among factors, the ANOVA results in Tables 4 and 5 should be interpreted sequentially. The terms in the tables were added in the order presented, and the F-tests were given for each term in sequence. In addition, an ANOVA model was evaluated where the area factor was added first. The result of that F-test was also highly significant (P of $F \leq 0.0001$). An examination of the residuals from the age-length and length-weight ANOVA models showed

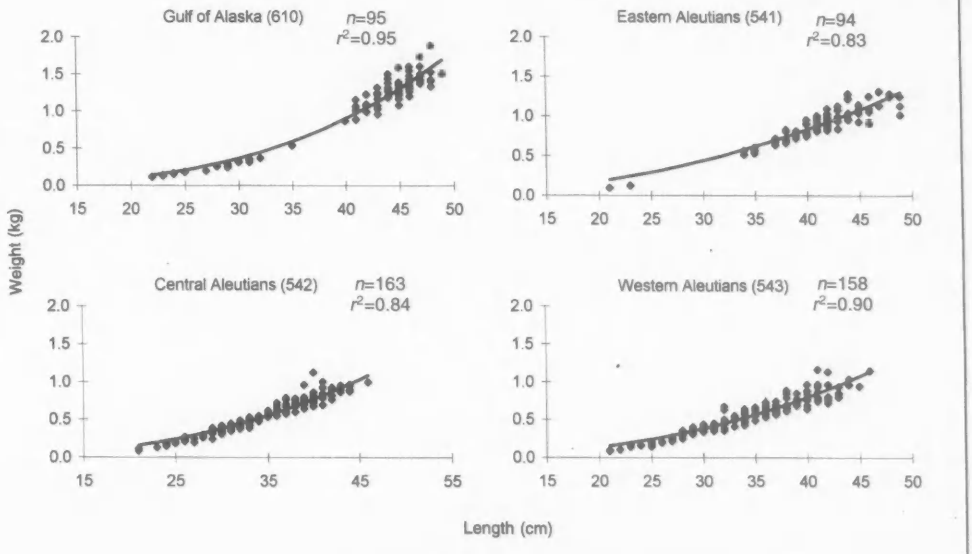
Gulf of Alaska (610) n=95 r²=0.95
Eastern Aleutians (541) n=94 r²=0.83
Central Aleutians (542) n=163 r²=0.84
Western Aleutians (543) n=158 r²=0.90
Weight (kg)
Length (cm)

Figure 3

Atka mackerel weight-length data by fishery management areas, collected from resource assessment surveys of the Gulf of Alaska and Aleutian Islands in 1993 and 1994, respectively. The fitted weight-length curves are plotted. Sample sizes (n) and the coefficients of determination (r^2) are given.

no obvious patterns, and the variances of the residuals were homogeneous by age and area, and by length and area, for the age-length and length-weight ANOVA models, respectively.

In order to evaluate the ANOVA model assumption of equality of variances among factors, the distributions of the raw length data by age within each area were examined, and the length distributions at age among areas were compared (Fig. 2), and suggested that the variances do not appear different. Examination of the distributions of the raw weight data by length within each area, and a comparison of the weight distributions at length among areas (Fig. 3), also suggested fairly homogeneous variances. It is noted that the ANOVA model is robust to small departures from the assumption of equal variances (Neter et. al, 1985).

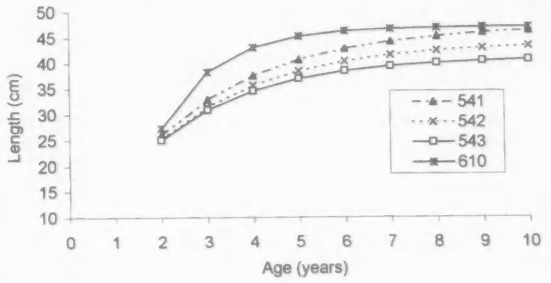

Figure 4

Estimated von Bertalanffy growth curves for Atka mackerel by fishery management area (541=eastern Aleutian, 542=central Aleutian, 543=western Aleutian Islands, and 610=western Gulf of Alaska) based on data collected from resource assessment surveys of the Aleutian Islands and Gulf of Alaska during 1993 and 1994, respectively.

Genetic data

Electrophoretic variation was observed at 30 of the 37 loci (Table 6). A majority of the variable loci (83%) had 2 to 4 alleles per locus. *IDHP-1**, *PEP-C**, and *PGK-1** had 5 alleles each, *AH-2** had 6 alleles, and *ADA** had 9 alleles. There were 14 $P_{0.95}$ loci; the frequency of the common allele at four of these loci (*ADA**, *AH-2**, *ALAT**, and *PEP-C**) was approximately 0.50.

One out of the 120 tests (0.8%) deviated from expected Hardy-Weinberg proportions (at the $P<0.05$ level) in the four samples. The Attu Island sample had an excess of heterozygotes for *ADA** ($P=0.013$).

When the four samples were pooled and tested as one population, none of the 30 tests of polymorphic loci deviated from expected Hardy-Weinberg proportions.

Average heterozygosity ranged from 0.135 to 0.142 (unweighted mean=0.136, Table 7) Percentage of polymorphic loci at the $P_{0.95}$ level ranged from 32.4% to 35.1%, and the mean number of alleles per locus ranged from 2.2 to 2.4. Seventeen unique, rare (frequency ≤0.01) alleles were identified; two each in Umnak Island and Attu Island, four in Kiska Island, and nine in Seguam Pass. Correlation of these alleles with sample size was 0.99.

Allele frequencies were similar for all samples for all polymorphic loci. The largest pair-wise allele frequency difference was 11.7% between Umnak Island (n=59) and Seguam Pass (n=96) for *ADA**100 (Table 3).[5] Only one of the 14 chi-square contingency tests for the $P_{0.95}$ loci was statistically significant (*AH-2**, P=0.004). The total chi-square was not statistically significant (P=0.08). Nei's unbiased genetic distance values ranged from 0.0000 to 0.00017 for the four samples. The mean F_{ST} for the 30 polymorphic loci was 0.004.

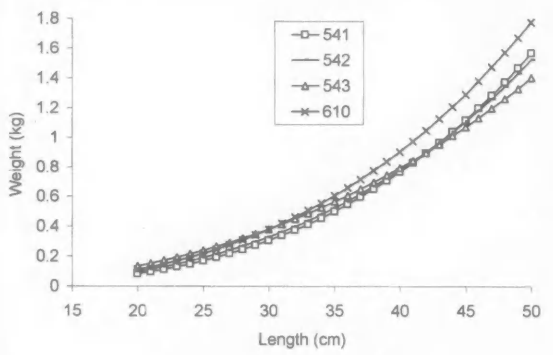

Figure 5

Estimated weight-length curves for Atka mackerel by fishery management area (541=eastern Aleutian, 542=central Aleutian, 543=western Aleutian Islands, and 610=western Gulf of Alaska) based on data collected from resource assessment surveys of the Aleutian Islands and Gulf of Alaska during 1993 and 1994, respectively.

Discussion

Growth and electrophoretic analyses

Analysis of variance showed that length-at-age and weight-at-age data were statistically different among the four management areas tested. In order to illustrate these differences, the age-length data were fitted to the commonly

[5] The power of this single locus pair-wise comparison is fairly high. For example, the probability of detecting a frequency difference of 0.15 between P_2 =0.40 and P_2 = 0.55 is 80% for samples consisting of 93 individuals each—similar to these samples sizes (Sokal and Rohlf, 1981). To be 90% certain of detecting such a difference, a sample of 122 individuals is needed.

Table 3

Parameter estimates from the von Bertalanffy growth equation (L_∞, K, t_0), and length-weight relationship (a, b), standard errors of the parameter estimates, mean square errors (MSE), and sample sizes (n) for the western Gulf of Alaska, eastern Aleutian, Central Aleutian, and Western Aleutian Islands.

	Gulf of Alaska		Eastern Aleutian Islands		Central Aleutian Islands		Western Aleutian Islands	
	Estimate	Standard error	Estimate	Standard error	Estimate	Standard error	Estimate	Standard Error
von Bertalanffy model								
L_∞	46.63	0.911	47.25	1.219	44.02	0.735	40.93	0.618
K	0.869	0.173	0.39	0.064	0.404	0.037	0.461	0.053
t_0	0.965	0.182	–0.041	0.389	–0.094	0.183	–0.05	0.247
MSE	5.98		5.36		3.44		6.52	
n	95		94		163		158	
Length-weight model								
a	0.859E-05	0.452E-05	0.237E-03	1.103E-04	0.878E-04	0.316E-04	0.652E-04	0.190E-04
b	3.132	0.137	2.212	0.123	2.46	0.098	2.55	0.08
MSE	0.01		0.01		0.01		0.01	
n	95		94		163		158	

Table 4

Two-way factorial analysis of variance of Atka mackerel length-at-age data collected from the 1993 and 1994 trawl surveys of the Gulf of Alaska and Aleutian Islands, respectively. The model contains the factors age and area, and an interaction term of age × area. SS = sum of squares.

Source	df	SS	Mean square	*F*-value	*P*>*F*
Age	11	14,576.45	1325.13	275.00	<0.0001
Area	3	5380.33	1793.44	372.19	<0.0001
Age × area	20	260.09	13.00	2.70	<0.0001
Error	477	2298.51	4.82		

Table 5

Two-way factorial analysis of variance of Atka mackerel length-weight data collected from the 1993 and 1994 trawl surveys of the Gulf of Alaska and Aleutian Islands, respectively. The model contains the factors length and area, and an interaction term of length × area. SS = sum of squares.

Source	df	SS	Mean square	*F*-value	*P*>*F*
Length	28	59.73	2.13	278.13	<0.0001
Area	3	1.21	0.40	52.77	<0.0001
Length × area	56	1.65	0.10	3.85	<0.0001
Error	425	3.26	0.01		

Table 6

Allele frequencies for 22 loci in Atka mackerel. "No." represents the number of successfully screened fish. Rare variation is described for 7 alleles[1] and 8 additional loci.[2] Seven loci were monomorphic: *AK**, *CK**, *bGALA**, *bGLUA**, *mMDH-2**, *sMDH-2**, and *PEPB-2**.

Locus, sample size and alleles	Sample location: Umnak Island	Seguam Pass	Kiska Island	Attu Island
*AAT-1**				
No.	39	100	73	74
*-100	1.000	0.995	0.993	0.993
*-63	0.000	0.005	0.007	0.007
*AAT-2**				
No.	62	100	80	73
*100	0.815	0.860	0.875	0.829
*60	0.185	0.135	0.112	0.164
*115	0.000	0.000	0.006	0.007
*82	0.000	0.005	0.006	0.000
*AAT-3**				
No.	70	89	76	73
*100	0.900	0.916	0.888	0.925
*110	0.100	0.084	0.112	0.075
*ADA**				
No.	59	96	78	72
*100	0.534	0.417	0.449	0.444
*75	0.280	0.292	0.269	0.285
*89	0.025	0.036	0.026	0.021
*110	0.008	0.031	0.064	0.049
*115	0.000	0.010	0.026	0.000
*120	0.110	0.172	0.135	0.174
*130	0.034	0.016	0.032	0.014
*140	0.000	0.010	0.000	0.000
*155	0.008	0.016	0.000	0.014
*ADH**				
No.	69	100	76	67
*-100	0.870	0.875	0.908	0.836
*-183	0.094	0.100	0.086	0.149
*-250	0.022	0.025	0.007	0.015
*-25	0.014	0.000	0.000	0.000
*AH-2**[3]				
No.	56	96	80	71
*100	0.536	0.521	0.613	0.514
*115[a]	0.384	0.354	0.300	0.366
*120	0.054	0.063	0.044	0.070
*117	0.009	0.000	0.019	0.014
*94	0.009	0.005	0.000	0.014
*84	0.009	0.057	0.025	0.021
*ALAT**				
No.	63	92	78	73
*100	0.563	0.533	0.564	0.555
*70	0.413	0.457	0.436	0.425
*120	0.024	0.011	0.000	0.021
*EST**				
No.	62	74	73	61
*100	0.645	0.608	0.541	0.648
*90	0.290	0.345	0.390	0.303
*110	0.040	0.041	0.062	0.033
*85	0.024	0.007	0.007	0.016
*G3PDH-1**				
No.	74	94	80	74
*-100	0.993	0.995	0.981	1.000
*-70	0.007	0.005	0.019	0.000
*G3PDH-2**[1]				
No.	72	98	67	74
*100	0.993	0.964	0.985	1.000
*125	0.007	0.031	0.015	0.000
*GPI-1**				
No.	73	100	80	74
*100	0.904	0.880	0.881	0.926
*25	0.096	0.120	0.119	0.074

continued

Table 6 (continued)

Locus, sample size and alleles	Sample location			
	Umnak Island	Seguam Pass	Kiska Island	Attu Island
IDDH[1]*				
No.	63	86	76	74
*100	0.984	0.948	0.954	0.973
*165	0.016	0.006	0.007	0.007
*25	0.000	0.041	0.039	0.020
*IDHP-1**				
No.	100	80	74	
*100	1.000	1.000	0.988	0.980
*65	0.000	0.000	0.000	0.007
*140	0.000	0.000	0.000	0.014
*MPI**				
*100	0.971	0.969	0.994	0.993
*110	0.014	0.020	0.006	0.007
*116	0.014	0.000	0.000	0.000
*90	0.000	0.010	0.000	0.000
PEPB-1[1]*				
n	74	90	80	74
*100	0.993	0.994	1.000	0.993
*90	0.007	0.000	0.000	0.007
No.	73	99	80	74
*100	0.562	0.576	0.544	0.500
*110	0.397	0.394	0.387	0.439
*118	0.007	0.005	0.019	0.034
*90	0.000	0.005	0.000	0.007
*113	0.034	0.020	0.050	0.020
*PEPD**				
No.	63	93	80	74
*100	0.738	0.742	0.794	0.804
*110	0.222	0.226	0.175	0.182
*120	0.024	0.011	0.025	0.014
*92	0.016	0.022	0.006	0.000
PGDH[1]*				
No.	69	99	79	72
*100	0.819	0.818	0.816	0.771
*80	0.152	0.152	0.152	0.153
*115	0.022	0.030	0.032	0.076
PGK-1[1]*				
No.	72	100	79	74
*100	0.785	0.765	0.829	0.770
*71	0.097	0.115	0.082	0.122
*45	0.097	0.090	0.082	0.101
*15	0.014	0.030	0.006	0.007
PGM[1]*				
No.	74	99	80	74
*100	0.926	0.960	0.944	0.953
*80	0.074	0.040	0.050	0.047
*SOD**				
No.	75	96	80	74
*100	0.993	0.964	0.981	0.993
*190	0.007	0.036	0.019	0.007
*TPI**				
No.	74	100	80	74
*-100	1.000	1.000	0.994	0.986
*-500	0.000	0.000	0.006	0.014

[1] Variation at alleles not listed above where the frequency of the allele is < 0.010: *G3PDH-2*90* and *IDDH*40* in Seguam Pass; *IDHP-1*90* and **50* in Kiska Island; *PEPB1*115* in Seguam Pass; *PGDH*70* and *PGK-1*55* in Gulf of Alaska; and *PGM*115* in Kiska Island.
[2] Variation at 8 loci not listed above where the frequency of the alternate allele is < 0.010: *AH-1*118* in Attu Island; *ENO*-180* in Seguam Pass; *FH*77*, and *GPI-2*93* , and **105* in Kiska Island; *IDHP-2*73* in Seguam Pass; *LDH*155* in Attu Island; *MDH-1*150* (*n*=100) and *PK*-350* in Seguam Pass.
[3] A seventh allele (**110*) could not be reliably distinguished from the **115* allele and therefore was pooled with the latter allele.

used von Bertalanffy curve, and the length-weight data were fitted to an allometric length-weight relationship. The *F*-tests on the growth curves determined that there was significant variability in the data among areas that was explained by separate growth curves rather than a single growth curve for all areas combined. Although the Gulf of Alaska and eastern Aleutian Islands data sets were small, data fits to the separate von Bertalanffy models were good, and an *F*-test indicated that separate growth curves were appropriate. There were low numbers of fish greater than five years in the Gulf of Alaska; however, the data set still allowed for fairly precise estimation of the asymptotic length (CV=0.02), the parameter most likely to be affected by the lack of older ages.

Morphological and meristic evidence and growth patterns suggest that Atka mackerel may have some degree of stock separation, at least by broad geographic areas (the eastern Bering Sea, Aleutian Islands, and Gulf of Alaska[1,2,3]; Lee, 1985; Kimura and Ronholt, 1988). The present study is the first genetic

Table 7

Within-sample genetic variability over 37 loci.

Location	Average heterozygosity	Percent of loci $P_{0.95}$	Average number of alleles/locus
Umnak Island	0.135	35.1	2.2
Seguam Pass	0.142	32.4	2.4
Kiska Island	0.135	35.1	2.3
Attu Island	0.137	32.4	2.2

survey of Atka mackerel intended to help understand the level and pattern of reproductive isolation among areas thought to be reflected in the areal growth differences. Samples of Atka mackerel were collected during the spawning season when groups of this species are locally aggregated, presumably providing the best separation of potentially reproductively isolated groups.

Our results show that Atka mackerel have above-average levels of genetic variation for a marine fish. The average heterozygosity per locus for Atka mackerel is 0.137, well above the average reported by Ward et al. (1994) for 57 species of marine fish (0.064 ± 0.004). Assuming that the majority of the allozyme variation is selectively neutral (Kimura, 1968), we believe that large levels of genetic variation are most parsimoniously explained by large, historically stable populations. An alternative explanation is that large levels of variability reflect a response to inhabiting a heterogeneous habitat (Avise, 1994). Nonetheless, 30 polymorphic loci provide substantial statistical power to assess the level of between-sample differentiation.

Between-sample variation was extremely low among the four samples of Atka mackerel. In a study where electrophoretic data for marine, freshwater, and anadromous fishes were compared, Ward et al. (1994) calculated an average G_{ST} (roughly equivalent to F_{ST}) of 0.062 for 57 species of marine fish (compared with 0.22 for freshwater species of fish). The F_{ST} for Atka mackerel (0.004) is far smaller than this average, providing evidence that a large amount of gene flow is occurring throughout the range represented by these samples. Very low genetic distance values between samples were observed; the largest distance value between two samples was 0.00017, indicating little or no stock differentiation. Furthermore, the nonsignificant Hardy-Weinberg test of the four samples pooled together did not indicate any between-sample heterogeneity. In light of these two genetic results, we can not reject the null hypothesis that our samples came from a single genetically homogenous population of Atka mackerel. There was also no apparent gradual differentiation throughout the Aleutian Archipelago corresponding to the clinal geographic variation seen in the growth data. Stock delineations based on the age-length and weight-length relationships were not supported by the allozyme data.

Concordance of electrophoretic and growth data sets

A lack of congruence between genetic and life history characteristics was also found for Pacific ocean perch by Seeb and Gunderson (1988). They analyzed data from the Washington coast to the Bering Sea. Stock delineations based on age structure, age-length relationships, and ages at maturity were not supported by the allozyme data. Although they did not find clear genetic stock differentiation, they did find a cline of gene frequencies within the Gulf of Alaska and significant allele frequency differences between the extremes of the geographic range for some loci.

There are at least three possible explanations for the lack of genetic stock differentiation for Atka mackerel in the Aleutian Islands. First, the genetic technique surveyed invariant gene loci when in fact genetic differences may exist among the sampled stocks. As in any genetic study, the absence of genetic differentiation does not preclude the possibility that true genetic differences exist, and other genetic techniques may be employed to further examine this possibility (Avise, 1994). Second, the species could perform a major spawning migration encompassing the entire population, with mixing and spawning in one area. Third, separate spawning locations are used but gene flow occurs among locations through the dispersal of pelagic larvae and juveniles. We consider the third explanation most likely given the growth differences seen in adult Atka mackerel.

The Aleutian Archipelago encompasses several wide and deep straits that could form barriers to significant movement across the island chain for adult demersal fish residing over the continental shelf. The pelagic behavior of larval and juvenile fish and their presumed distribution in the open ocean habitat, however, would make them susceptible to wide dispersal by currents, thus accounting for the genetic homogeneity among samples. A schematic diagram of the basic surface currents in the north Pacific is shown in Figure 6 (McAlister and Favorite, 1977). The Alaska stream flows westward throughout the Aleutian Archipelago, with significant northward flow to the Bering Sea through Amukta, Amchitka, and Buldir passes. The North Aleutian current flows eastward to Umnak Island providing a thorough mixing mechanism across the Aleutian Island chain. The currents could thus provide the mechanism for sufficient gene flow through the Aleutian chain to actually prevent genetic differentiation. It is presumed that adults do not undertake large-scale migrations and assume a fairly localized existence, which might thus account for the differences in length, age, and weight comparisons of the adults. Observed spawning areas in the Aleutian, Shumagin, and Commander Islands, which have been historically referenced in the literature (Turner, 1886; Rutenberg, 1962), are thus presumed to attract nearby resident schools that migrate inshore.

Although there are no major currents flowing eastward from the Aleutian Islands to the Gulf of Alaska,

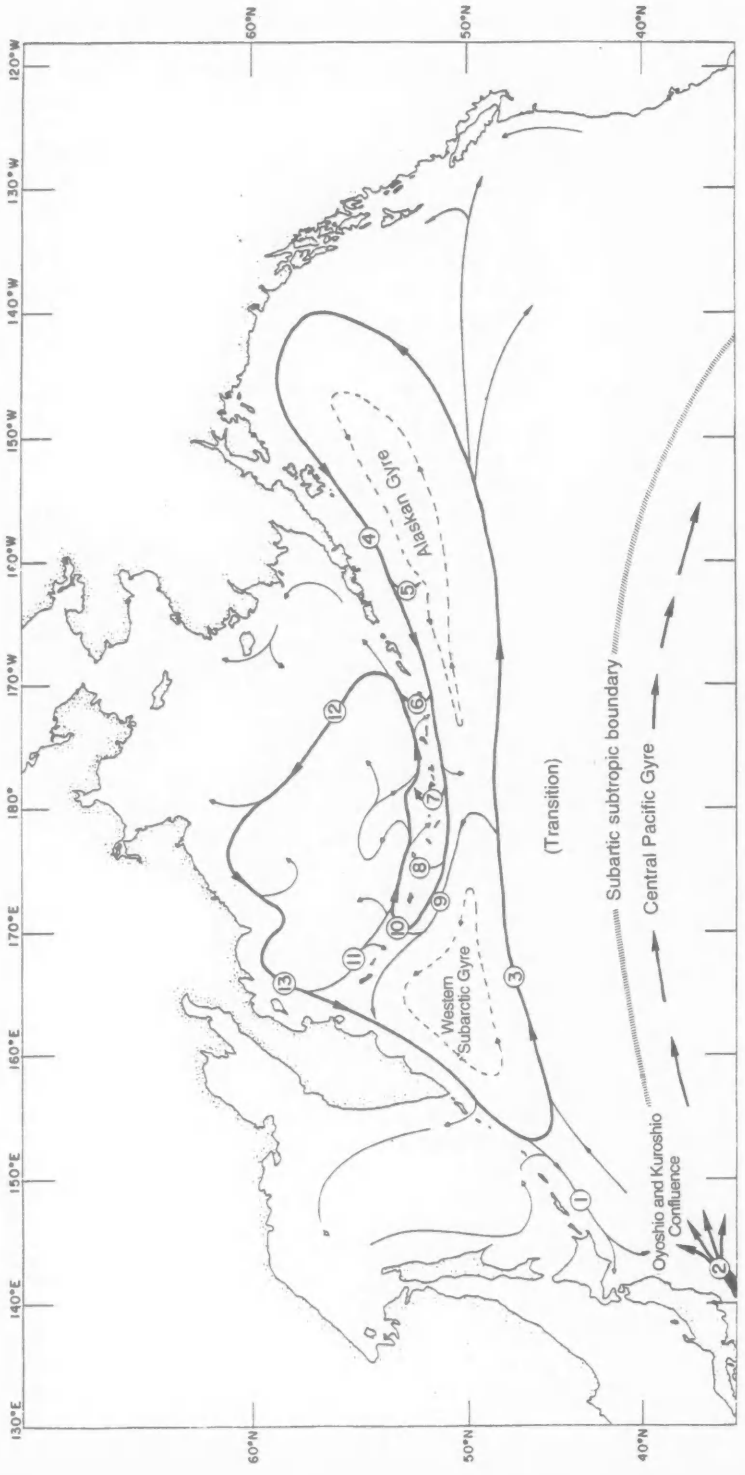

Figure 6

Subarctic Pacific region showing the western subarctic gyre and the Alaskan gyre within the subarctic gyre and associated currents. Numbers refer to currents: 1 = Oyashio; 2 = Kuroshio; 3 = subarctic; 4 = Alaskan Stream; 5 = Aleutian; 6 = Amukta; 7 = Amchitka; 8 = Buldir; 9 = west subarctic; 10 = Near; 11 = Commander; 12 = Transverse; and 13 = East Kamchatka (as presented by McAlister and Favorite, 1977).

the western Gulf of Alaska portion of the population may be the result of juvenile or adult migration (or both) or habitat expansion. Kimura and Ronholt (1988) postulated that Gulf of Alaska Atka mackerel are at the extreme limit of their geographic range (the extreme limit of which is populated only during periods of favorable environmental conditions).

Zolotov (1984) found that Atka mackerel spawning habitat in Russian waters extended from the Kamchatka Peninisula through the Kurile Islands almost without breaks. Continuous distribution of Atka mackerel spawning habitat and dispersal of larvae into the open ocean pointed to an absence of mechanisms that would result in reproductively isolated stocks in Russian waters. Zolotov (1984) thus concluded that Atka mackerel did not form ecological groupings along the Kamchatka Peninsula and Kurile Islands but made up a single population. Although we cannot rule out that there are unknown mechanisms or processes which might result in reproductive isolation of groupings of Aleutian Island Atka mackerel, life history information suggests that a process for extensive mixing occurs during the early life stages. We currently do not have any observations to support the necessary processes (e.g. larval retention, natal homing, genetic imprinting), that would result in reproductive isolated populations in the Aleutian Islands.

We interpret the areal growth differences exhibited by Atka mackerel as indications of localized assemblages made up of groupings from a single mixing stock that aggregates during the adult portion of its life history. We suggest that the local specific growth variability seen in adults is a reflection of environmental effects. It is unknown which environmental characteristics might be most influential on growth of Atka mackerel; however, temperature and salinity are noted to be the most important hydrological factors affecting the distribution of hexagrammids, and food, predators, and parasites the most important biological factors (Rutenberg, 1962). Seeb and Gunderson (1988) noted that local growth and age-at-maturity differences could also reflect historical influences and fishing pressure. A large and sustained Atka mackerel fishery has been conducted throughout the Aleutian Islands since the early 1970s. Catches have fluctuated with the demise of the foreign fishery and the development of the domestic fishery, and in recent years the fishery has been concentrated in the eastern Aleutian Islands where the largest fish reside. The fish in the western Aleutian Islands were not heavily exploited from 1980 to 1994, but they have historically been the smallest fish. The geographic size cline noted in the growth data seems to run counter to what we might expect given the differential fishing pressure.

Stock assessment and management implications

The stock structure of Atka mackerel has stock assessment and fishery management implications. From a stock assessment perspective, we are interested in elucidating the underlying population processes that would result in stock separation, or lack of, and in evaluating the impacts of the fishery on the genetic stock(s), particularly on the spawning concentrations. From a fishery management perspective, the practical recognition of fishery-targeted assemblages (not necessarily genetically distinct) and the spatial and temporal affects of harvesting these assemblages are of interest.

Historically, small-scale Alaskan subsistence fisheries targeted spawning concentrations of Atka mackerel, but the very shallow and presumably rough habitat of the spawning grounds are not accessible to the current large-scale commercial fisheries. Analysis of commercial fishery data indicates that bottom trawling is probably not disturbing the nesting sites.[6] Thus, the unique reproductive life history features of Atka mackerel may provide for some protection of the spawning stock.

Booke (1981) distinguished between inherited (genetic) versus "acquired" or "environmentally induced" characters; the latter including morphological and phenotypic characteristics. Because acquired phenotypic markers by definition are appropriated through contact with the environment, they may not reflect the population genetic characteristics (Avise, 1994). However, acquired markers can serve an important role in population analysis because they can reveal where individuals have spent various portions of their lives (Avise, 1994). From both a stock assessment and fishery management perspective, the localized aggregations of adult Atka mackerel, although not genetically distinct, are important to our understanding of the population dynamics of this species and the impact of the fishery.

Indications of localized populations of Atka mackerel raise the issue of potential localized depletion by the fishery. Another fundamental fishery management and assessment question has been the relation of Gulf of Alaska Atka mackerel to Aleutian Islands Atka mackerel. Atka mackerel are currently managed by two major areas, the Gulf of Alaska and the Aleutian Islands, and by three subareas within the Aleutian Islands. For management purposes, there are at least two catch quotas that must be set given the management area boundary at 170°W which divides the Gulf of Alaska and the Aleutian Islands. Any further subdivisions of the quota are generally based on stock separation rationale or the desire to spread out fishing effort over large geographic areas (or both). The Gulf of Alaska Atka mackerel are assessed separately from Aleutian Islands Atka mackerel, mainly because of the different sources of data (two different survey time series), and to a lesser extent on the presumption that Gulf of Alaska Atka mackerel showed some level of separation from Aleutian Islands Atka mackerel. The results of this study show no evidence of Atka mackerel genetic stock separation between the western Gulf of Alaska and throughout the Aleutian Islands chain. However, because adults show evidence of localized aggregations, it seems appropriate to set at least two separate quotas in Alaskan waters (Gulf of Alaska and Aleutian Islands), with further subdivisions to distribute fishing effort.

The North Pacific Fishery Management Council (NPFMC) implemented Amendment 28 to the "Fishery Management Plan for the Groundfish of the Bering Sea and Aleutian Islands," creating three subareas within the large Aleutian Islands management area (Fig. 1). The impetus for the implementa-

[6] Fritz, L. W., and S. A. Lowe. 1997. Seasonal distributions of Atka mackerel (*Pleurogrammus monopterygius*) in commercially-fished areas of the Aleutian Islands and Gulf of Alaska. NMFS. Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115-0070. Unpubl. manuscript.

tion of additional management areas was the possibility of localized depletion of Atka mackerel by the fishery given the presumed localized distribution of this species and the localized, highly concentrated fishery effort. This study shows that genetically distinct populations of Atka mackerel do not exist in this area, and therefore a significant amount of gene flow may occur among locales within this species. However, gene flow is presumably occurring during the early life stages (larval, juvenile) and is dependent on dispersal by currents. The potential for localized depletion by the fishery at the adult stage is still a concern. Until we have a better understanding of the dispersal and distribution mechanisms affecting Atka mackerel early life stages, management strategies should strive to spread out fishing effort to help reduce the potential for localized depletion. We conclude that despite the genetic homogenization, the phenotypic variation in adult Atka mackerel warrants consideration by fishery managers.

Acknowledgments

We acknowledge the field biologists on surveys who accommodated our sampling plan and painstaking collected the biological samples, in particular, Bill Flerx, Michael Martin, and Robin Harrison. This work would not be possible without their efforts. We also thank David Kuligowski for his laboratory assistance in processing the genetic samples and Lowell Fritz, Dan Kimura, Anne Hollowed, and three anonymous reviewers, whose reviews of our manuscript improved it considerably.

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A population profile for hagfish, *Myxine glutinosa*, in the Gulf of Maine. Part 2: Morphological variation in populations of *Myxine* in the North Atlantic Ocean

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Abstract.—The species *Myxine glutinosa* has long been recognized as encompassing both eastern and western North Atlantic populations. Wisner and McMillan (1995) have proposed splitting the species into *M. limosa* (Girard, 1858; western North Atlantic) and *M. glutinosa* (Linnaeus, 1758; eastern North Atlantic). We examined a variety of morphological characteristics, including cusp counts, slime pore counts (total, prebranchial, trunk, and tail), total length, and body proportions (prebranchial, trunk, and tail length, maximum width and depth, and depth at cloaca). Several western Atlantic populations of varying size were compared with one large sample from the waters between Sweden and Denmark. The results indicate that although specimens from the Gulf of Maine differ significantly from those collected in the eastern North Atlantic, specimens collected from the mid-Atlantic coastal region of the United States and from northern Canadian waters are less distinctive. In addition, there are significant morphological differences among the populations sampled in the western North Atlantic. It is therefore suggested that until and unless molecular data indicate otherwise, the species name *M. glutinosa* be retained as encompassing both eastern and western North Atlantic populations.

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Only one hagfish, *Myxine glutinosa* (Linnaeus, 1758), has been found on both sides of the North Atlantic Ocean; this is the only hagfish reported from within the Gulf of Maine. *Myxine glutinosa* are an important species in the Gulf of Maine because 1) they are present in substantial numbers (densities may reach 500,000/km^2), and they may have a considerable impact on the benthic community (Lesser et al., 1996; Martini et al., 1997b), 2) they have direct and indirect effects on commercial fisheries in the Gulf of Maine, through predation on groundfish in fixed gear fisheries and through competition for shrimp, and 3) they have commercial value as the basis for a leather fishery that provided Gulf of Maine fishermen with $1.2 million in 1996.

The first part of this study (Martini et al., 1997a) presents morphological data and a population profile for hagfish in the inner Gulf of Maine. In this report we compare the morphological characteristics of this population with those of *M. glutinosa* populations in other geographical regions. Wisner and McMillan (1995) proposed splitting *M. glutinosa* into *M. glutinosa* (Linnaeus, 1758) for the eastern North Atlantic (ENA) and *Myxine limosa* (Girard, 1858) for the western North Atlantic (WNA). The proposed separation was based on differences in size at sexual maturity, maximum size, and the color of preserved specimens. We undertook this analysis initially to see if there were significant morphometric differences that would support the separation of species. This ultimately led us to perform statistical comparisons among our morphological data, collected in the inner portion of the Gulf of Maine, and the data of other researchers working with eastern and western North Atlantic populations of *M. glutinosa*.

Materials and methods

Wisner and McMillan included morphometric data for *Myxine* collected over a very broad area. The latitudinal limits were 33°46'N to 66°39'N, and the longitudes ranged from 79°42'W to 52°13'W. Of the 138 specimens cited in their report, only 28 (20%) were collected within the boundaries of the Gulf of Maine. Their study provided detailed data

on the numbers of slime pores (prebranchial, trunk, tail, and total) and total cusp counts for *Myxine* in the eastern and western North Atlantic. Through correspondence with Robert L. Wisner,[1] we obtained data and collection information for 73 western North Atlantic (WNA) and 179 eastern North Atlantic (ENA) specimens. These data sets permitted extensive comparisons with our morphological data for 1478 specimens from the inner Gulf of Maine (WNA).

Methods of measuring and counting followed those of Fernholm and Hubbs (1981) and McMillan and Wisner (1984). The body axis was divided into prebranchial, trunk, and tail regions. The prebranchial measurement extends from the tip of the snout to the anterior margin of the pharyngocutaneous duct (pcd), the trunk continues to the anterior margin of the cloaca, and the tail region extends from that point to the tip of the tail. The sum of these measurements is equal to the total length (TL). The proportional measurements were recorded in millimeters and converted to percentages of total length. Additional data included body depth, body width, cloacal depth, and tail depth (in mm and %TL); total slime pore count (TP) with prebranchial, trunk, and tail counts (as values and %TP), and total cusp counts.

Morphological data were collected from 306 hagfish from the inner Gulf of Maine during five years of trap surveys at depths of 120–150 m by staff and students of the Shoals Marine Laboratory. Samples were collected from late June to early September. The traps used in this study were comparable to those set by the commercial hagfishing fleet. The trap used on most trips consisted of a weighted garbage can with 5–7.5 cm holes in the side and an inner, baited trap of wire screening. After collection, the animals were transferred to tanks of chilled seawater (2–6°C) at 32–35 ppt salinity for transport to the marine laboratory. All measurements were taken on fresh specimens. Total length data from these samples were combined with length data provided by the New England Fisheries Development Association for 1172 hagfish collected by fishermen within 80 km of the shoreline in the southern Gulf of Maine over the period of June–July 1995. All specimens were collected at depths of 120–180 m.

Samples from elsewhere in the North Atlantic were collected by either trawling or trapping at depths of 30–600 m between 1965 and 1987 (Wisner[1]). Collections in the eastern North Atlantic were from midsummer (August); those from the western North Atlantic were from all seasons. The morphological data from these collections were recorded from preserved specimens by Robert L. Wisner and Charmion McMillan. An analysis of variance was performed on the data with the fixed effect of collection site by using Statview 4.5 (Abacus Concepts Inc., 1995). This analysis consisted of post-hoc multiple comparison tests (Scheffe *F*-test) at the 5% level of significance.

Results

When plotted out on regional charts (Fig. 1), the data

[1] Wisner, R. L. 1996. Marine Biology Research Division, Univ. California, San Diego, La Jolla, CA 92093-0202. Unpubl. data.

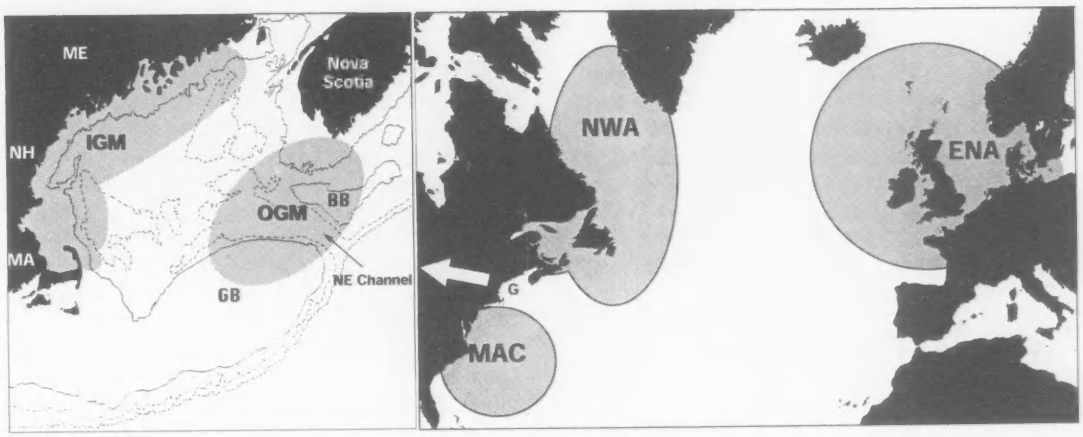

Figure 1

Sampled populations of *M. glutinosa* in the eastern and western North Atlantic. The shaded areas indicate the approximate range of collection sites for each data set. (**Left**) Collection sites within the Gulf of Maine. The 100-m, 200-m, and 300-m depth contour lines are indicated. OGM = outer Gulf of Maine; IGM = inner Gulf of Maine; BB = Brown's Bank; GB = George's Bank (**Right**) Other collection sites in the North Atlantic. ENA = eastern North Atlantic; NWA = Northwest Atlantic; G = Gulf of Maine (see [left]); and MAC = mid-Atlantic coast.

Table 1

Morphological measurements for *Myxine glutinosa* in the eastern and western North Atlantic. Asterisks indicate values significantly different ($P<0.0001$) from the Eastern Atlantic population.

Character	Mean	SD	Range	%TL[1]	SD	Range	*n*
Eastern North Atlantic group (ENA)							
Total length (mm)	299	31	227–387	100			179
Prebranchial (snout:pcd)	82	8	61–101	27.4	1.1	24–31	179
Trunk	174	20	133–227	58.2	1.5	54–62	179
Tail	44	5	33–59	14.9	0.9	12–18	179
Width	14	2	10–21	4.9	0.5	3–6	179
Depth (trunk)	18	3	13–26	6.1	0.6	5–8	179
Depth (cloaca)	14	2	10–20	4.7	0.5	4–7	179
Depth (tail)	15	2	12–20	5.1	0.4	4–6	179
Inner Gulf of Maine group (IGM)							
Total length (mm)[2]	524*	102	170–950	100			1478
Prebranchial (snout:pcd)	135	27	54–200	26.7*	1.6	24–37	143
Trunk	311	72	28–459	61.4	5.9	42–83	143
Tail	64	14	25–106	12.6*	1.2	9–17	143
Width	14	7	4–35	2.7*	1.1	2–6	91
Depth (trunk)	22	7	8–35	4.2*	0.7	2–7	87
Depth (cloaca)	19	5	6–28	3.7*	0.5	2–5	198
Depth (tail)	20	5	8–30	4.0*	0.5	2–5	97

[1] %TL = Percentage of total length. Values were log-transformed before comparison.
[2] Combined data, from Martini et al., 1997a, and Kuenstner, 1996.

collection sites fell into four groups: 1) mid-Atlantic coast (MAC), from the latitude of Charleston, South Carolina, to the southern coast of New England (n=51, with data on total length, slime pore counts, and cusp counts), 2) the outer Gulf of Maine (OGM), from the area of Brown's Bank (n=13, with data on total length, slime pore counts, and cusp counts), 3) the northwestern Atlantic (NWA) off Labrador, including Davis Strait (n=9, with data on total length, slime pore counts, and cusp counts), and 4) the eastern North Atlantic (ENA), from the Skaggerrack, between Sweden and Denmark (n=179, data on total length, proportional lengths, slime pore counts, and cusp counts). Our data set comprised a separate group, 5) the inner Gulf of Maine (IGM), represented by samples from within 80 km of the shoreline (n=1478 for total lengths, n=143 for proportional measurements, n=94–97 for slime pore counts and cusp counts).

Comparisons of morphometric data for the ENA and IGM populations, the two groups for which the greatest number of measurements were available, showed differences in total length and proportional measurements (Table 1). Table 2 presents data on cusp counts and slime pore counts for all groups (NWA, IGM, OGM, MAC, and ENA). The proportional measurements expressed as %TL and %TP were log-transformed before analysis and retransformed for presentation in the tables. Figure 2 illustrates the results of the post-hoc multiple comparison tests (Scheffe F-test) at the 5% level of significance. Table 3 details these results. Table 4 compares the data on total length for the sampled populations.

These results can be briefly summarized as follows:

1 The NWA sample, closest geographically to the ENA population, can be distinguished from the ENA only in terms of the trunk slime pores as a percentage of the total slime pore count. The total length data for the NWA and ENA groups are not significantly different.
2 The NWA sample is distinct from the OGM sample in terms of the total slime pore count and differs from the IGM sample with regard to prebranchial, trunk, and total slime pore counts as well as the total cusp count. The differences in regional slime pore count between the NWA and IGM samples were not significant when compared as percentages of the total slime pore count.
3 The OGM sample differs from the ENA sample in terms of the total slime pore count, and from the IGM sample in terms of the trunk slime pore count (as a value, not as a percentage of total slime pores) and in the total slime pore count. The total length data for the OGM and ENA groups were not significantly different, but the OGM animals were significantly smaller than those of the IGM.
4 The mid-Atlantic coastal group (MAC) has characters that overlap those of other groups. The MAC

Table 2

Tooth cusp counts and slime pore counts for populations of *Myxine glutinosa* L. in the eastern and western North Atlantic. Parenthetical values refer to the data expressed as a percentage of the total number of slime pores.

Character	Population	Mean	SD	Range	*n*
Total cusp count	NWA	32	1	31–34	9
	OGM	35	2	33–39	7
	IGM	35	2	28–40	97
	MAC	35	2	30–38	51
	ENA	34	1	29–38	101
Total slime pore count	NWA	95	2	91–101	9
	OGM	106	4	100–113	13
	IGM	114	7	91–128	94
	MAC	100	4	91–108	51
	ENA	96	5	85–108	143
Prebranchial slime pores (%)	NWA	26 (27)	3 (2)	23–32 (25–29)	9
	OGM	31 (29)	1 (1)	28–32 (28–30)	13
	IGM	33 (29)	4 (3)	20–45 (21–40)	94
	MAC	28 (28)	2 (2)	25–33 (25–33)	51
	ENA	27 (28)	3 (2)	20–36 (24–33)	143
Trunk slime pores (%)	NWA	58 (61)	3 (1)	56–66 (59–62)	9
	OGM	63 (59)	2 (1)	59–67 (57–61)	13
	IGM	67 (59)	4 (3)	51–77 (51–69)	94
	MAC	59 (59)	2 (2)	54–65 (55–64)	51
	ENA	56 (58)	3 (<0.5)	50–63 (57–60)	143
Tail slime pores (%)	NWA	11 (12)	1 (2)	8–13 (8–14)	9
	OGM	13 (12)	1 (1)	11–15 (10–14)	13
	IGM	13 (11)	2 (1)	8–19 (9–15)	94
	MAC	12 (12)	1 (1)	10–14 (10–14)	51
	ENA	12 (13)	1 (1)	8–15 (9–14)	143

data and the NWA sample differ significantly in the total cusp count. The MAC sample differs from the OGM sample in terms of the total slime pore count; it differs from the IGM sample in terms of prebranchial, trunk, tail, and total slime pore counts; the regional differences are not significant when compared as percentages of the total slime pore count. The MAC sample differs from the ENA sample in the trunk slime pore count (as a value, not as a percentage of total slime pores) and total cusp count. The total length data for the MAC, OGM, and ENA groups are not significantly different; all are significantly smaller than the IGM animals.

5 The IGM data is distinct from the ENA group for trunk, tail, and total slime pore and cusp count data. The IGM and ENA groups also differ significantly in prebranchial, trunk, and tail lengths, body width, body depth, tail depth, and cloacal depth (as percentages of total body length).

6 Hagfish from the inner Gulf of Maine were significantly larger than hagfish collected in any other location ($P<0.0001$). The average lengths of the OGM and MAC samples (315 mm and 280 mm respectively) were not significantly different from that of the ENA population (290 mm; see Tables 4 and 5). Further, we are unaware of any records for *M. glutinosa* larger than 450 mm outside of the Gulf of Maine or the adjacent continental slopes. Wisner and McMillan (1995) reported total lengths of 117–501 mm for their WNA sample (n=78). With deletion of the 13 animals known to be from the outer Gulf of Maine, the size range becomes 117–446 mm. This range, which still includes 15 animals from the outer Gulf of Maine,[2] is within the size range reported for eastern North Atlantic *M. glutinosa* (maximum size of 450 mm. It may also be significant that one of the OGM specimens, 350 mm in total length, contained fully mature eggs (SI075-689, from 42°40.5' N, 66°37'W; Wisner[1]). This is above the size of sexual maturity for eastern North Atlantic *M. glutinosa* (200 mm) but below the apparent length at maturity for specimens in the IGM sample (400 mm; Martini et al., 1997a). The large maximum size and large size at maturity

[2] Data forms did not permit determination of individual sizes, only ranges for these collection sites.

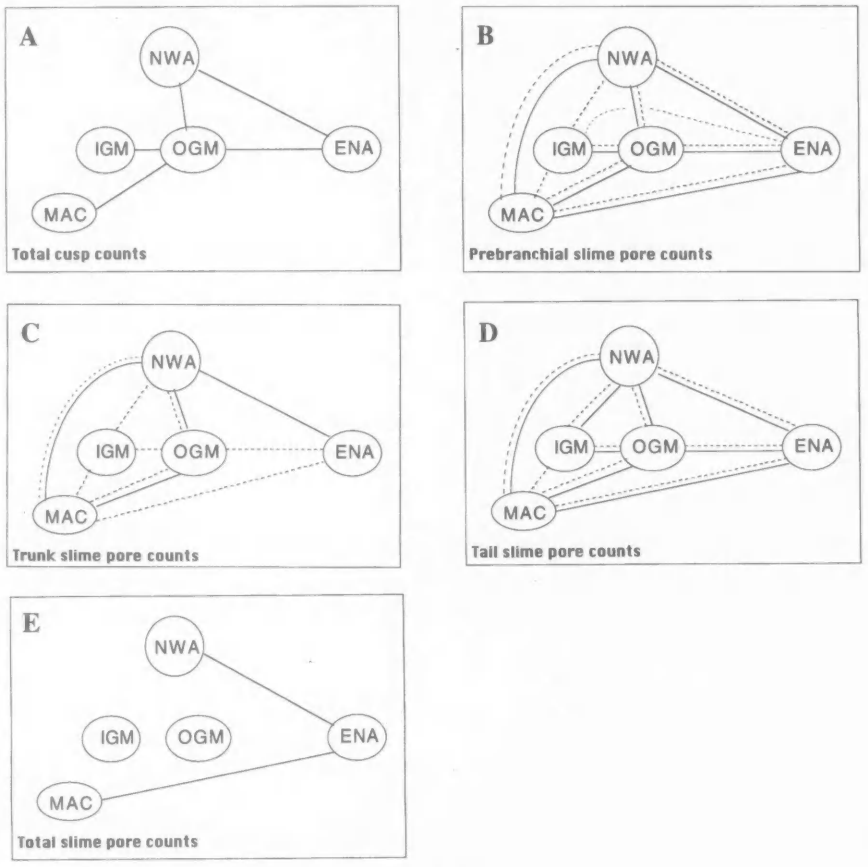

Figure 2

Relationships among the sampled populations of *M. glutinosa* for cusp counts and slime pore counts. A solid line connecting two populations indicates no significant difference exists between the absolute values. A dashed line indicates no significant difference exists between the values expressed as percentages of the total slime pore counts. (**A**) Total cusp counts; (**B**) prebranchial slime pore counts; (**C**) trunk slime pore counts; (**D**) tail slime pore counts; (**E**) total slime pore counts. NWA = Northwest Atlantic; IGM = inner Gulf of Maine; OGM = outer Gulf of Maine; ENA = eastern North Atlantic; and MAC = mid-Atlantic coast.

that has been widely attributed to *M. glutinosa* in the western North Atlantic thus appears to be valid only for the inner Gulf of Maine.

In summary, the IGM group is significantly larger in total length than any other population sampled. Proportional measurements could be compared only between the IGM and ENA samples. In addition to having much greater total length, hagfish from the IGM sample are more slender (both in width and depth) and have shorter prebranchial segments and shorter, narrower tails than ENA specimens. Allometric effects are probably not responsible for these differences, which remain significant even when the IGM data set is restricted to animals of the same size range as that in the ENA sample (<400 mm). Total length, slime pore counts, and total cusp counts could be compared among all groups. The highest variability observed was in the total slime pore count. Specimens from the Gulf of Maine (IGM and OGM) differed from one another and from all other sample groups. In terms of the regional distribution of slime pores, there were significant differences between the IGM and ENA samples when compared as absolute values or as percentages of the total slime pore count. Differences in the regional distribution of slime pores

Table 3

Results of post-hoc multiple comparison tests (Scheffe *F*-test) at the 5% level of significance. For counts, means, and standard deviations, refer to Table 2. The asterisks (*) indicate values significant at the 5% level (Scheffe *F*-test).

Groups compared	Mean diff.		*P*-value	
Prebranchial slime pore counts, as value and percentage of total (in parentheses)				
IGM vs. MAC	5.216	(0.020)	<0.0001*	(0.4127)
IGM vs. NWA	7.517	(0.033)	<0.0001*	(0.1905)
IGM vs. OGM	2.756	(0.005)	0.2380	(0.9979)
IGM vs. ENA	6.045	(0.014)	<0.0001*	(0.0915)
MAC vs. NWA	2.301	(0.019)	0.7105	(0.8340)
MAC vs. OGM	−2.46	(0.009)	0.4471	(0.9913)
MAC vs. ENA	.828	(−0.010)	0.8798	(>0.9999)
NWA vs. ENA	−1.472	(−0.019)	0.9448	(0.8091)
OGM vs. NWA	4.761	(0.028)	0.0865	(0.6534)
OGM vs. ENA	3.288	(0.009)	0.0661	(0.9849)
Trunk slime pore counts as value and percentage of total (in parentheses)				
IGM vs. MAC	8.550	(0.002)	<0.0001*	(0.9985)
IGM vs. NWA	9.197	(−0.017)	<0.0001*	(0.2559)
IGM vs. OGM	4.838	(0.004)	0.0022*	(0.9985)
IGM vs. ENA	11.170	(0.010)	<0.0001*	(0.0212)*
MAC vs. NWA	0.647	(−0.019)	0.9997	(0.2076)
MAC vs. OGM	−3.712	(0.002)	0.0861	(>0.9999)
MAC vs. ENA	2.619	(0.008)	0.0030*	(0.3125)
NWA vs. ENA	1.972	(0.027)	0.8591	(0.0054)*
NWA vs. OGM	−4.359	(0.022)	0.2478	(0.2986)
OGM vs. ENA	6.331	(0.006)	<0.0001*	(0.9760)
Tail slime pore counts as value and percentage of total (in parentheses)				
IGM vs. MAC	0.995	(−0.006)	0.0166*	(0.0694)
IGM vs. NWA	1.655	(−0.005)	0.1012	(0.9683)
IGM vs. ENA	0.794	(−0.012)	0.0088*	(<.0001)*
IGM vs. OGM	−0.276	(−0.010)	0.9987	(0.0694)
MAC vs. NWA	0.660	(0.001)	0.9538	(0.9995)
MAC vs. OGM	−1.271	(−0.004)	0.2460	(0.9376)
MAC vs. ENA	−0.201	(−0.006)	0.9940	(0.1040)
NWA vs. ENA	−0.861	(−0.007)	0.8116	(0.6125)
NWA vs. OGM	−1.932	(−0.006)	0.1156	(0.9204)
OGM vs. ENA	1.075	(−0.001)	0.3745	(>0.9999)
Total slime pore counts				
IGM vs. MAC	14.227		<0.0001*	
IGM vs. NWA	18.429		<0.0001*	
IGM vs. OGM	7.566		0.0039*	
IGM vs. ENA	17.38		<0.0001*	
MAC vs. NWA	4.203		0.6730	
MAC vs. OGM	−6.661		0.0353*	
MAC vs. ENA	3.154		0.0922	
NWA vs. OGM	−10.863		0.0054*	
NWA vs. ENA	−1.076		0.9995	
OGM vs. ENA	9.787		<0.0001*	
Total cusp counts				
IGM vs. MAC	0.432		0.9625	
IGM vs. NWA	3.409		0.0006*	
IGM vs. OGM	0.235		>0.9999	
IGM vs. ENA	1.883		<0.0001*	
MAC vs. NWA	2.978		0.0109*	
MAC vs. ENA	1.667		0.0003*	
MAC vs. OGM	−0.197		>0.9999	
NWA vs. ENA	−1.310		0.7119	
NWA vs. OGM	−3.175		0.1263	
OGM vs. ENA	1.864		0.4313	

between the groups IGM-MAC, IGM-NWA, IGM-OGM, and MAC-ENA were not significant when compared as percentages of the total slime pore count. Total cusp counts differed significantly between NWA-IGM, NWA-MAC, IGM-ENA, and MAC-ENA.

Discussion

The primary goal of this analysis was to assess the validity of the proposed splitting of *M. glutinosa* L. into two species. With the exception of the IGM data, the proposal by Wisner and McMillan (1995) was based on a general morphological comparison of animals collected from the eastern and western North Atlantic. This study used their data, assigned to the NWA, OGM, MAC, and ENA groups. As is often the case when working with fishes whose lifestyles, habits, and population dynamics are poorly understood, there are a number of potential complicating factors that could bias these data. For example, both the Wisner and McMillan study and our own have compared specimens collected by 1) different methods, 2) at different times, and 3) at different depths. This is not unusual; the majority of the 59 currently recognized species of hagfishes are known from small numbers of animals (often just one) caught accidentally in mobile fisheries gear. The limitations of our data sets are therefore shared not just with Wisner and McMillan (1995) but with many other studies of hagfish systematics. Our goal was to determine if—given the limitations of the available data—the proposed split could be justified on the basis of the available morphological data.

We will now discuss each of these complicating factors as they influence hagfish collections in general, and the data in this study in particular.

The collection method might affect the size range of animals captured

Comparative data on trawl versus trap collection of *Myxine* are unavailable, but it is known that trawl-

Table 4

Size distribution in populations of *Myxine glutinosa* in the eastern and western North Atlantic. Total length measurements (in mm) reported for eastern and western Atlantic populations (all groups). See text for explanation of abbreviations.

	NWA	OGM	IGM	MAC	ENA
		315	509	280	299
Average range	190–405 (n=11)[1]	215–510 (n=13)[1]	195–724 (n=306)[3]	220–380 (n=13)[1]	227–392 (n=179)[1]
			529		312
		103–405 (n=8)[2]	170–950 (n=1172)[4]	220–420 (n=37)[2]	253–362 (n=8)[5]
					<450[6]

[1] From Wisner and McMillan (1995).
[2] From raw data provided by R. Wisner (see Footnote 1 in main text).
[3] From Martini et al. (1997a).
[4] From Kuenstner (1996).
[5] From Fernholm (1981).
[6] From Adams and Strahan (1963).

Table 5

Results of post-hoc multiple comparison tests of total lengths; asterisks (*) indicate values significant at the 5% level (Scheffe F-test). See text for explanation of abbreviations.

Groups compared	Mean difference	P-value
IGM vs. MAC	231.490	<0.0001*
IGM vs. NWA	213.798	<0.0001*
IGM vs. OGM	196.381	<0.0001*
IGM vs. ENA	213.099	<0.0001*
MAC vs. NWA	–17.692	0.9996
MAC vs. OGM	35.109	0.9698
MAC vs. ENA	–18.391	0.9943
NWA vs. ENA	–1.217	>0.9999
NWA vs. OGM	–17.417	0.9996
OGM vs. ENA	16.718	0.9904

ing estimates of hagfish population density produce gross underestimates (Wakefield, 1990). Given the maximum swimming rate of adult *Myxine* (<1 m/sec, Foss, 1968), hagfish of any size are probably unable to outrun a trawl. We would predict that trapping would collect smaller individuals that might slip through the trawl mesh, whereas trawling could collect mature animals that might not be attracted to traps (breeding hagfish may not feed; Walvig, 1963). However, because we have no indication of allometric effects of body size on any morphometric character for *M. glutinosa*, the statistical comparisons of slime pore counts, cusp counts, or proportional measurements should be unaffected by variations in total length among the sample populations. Neither traps with large-bore entrances or trawl nets, the collection methods used for these data, should bias the maximum recorded size.

Collections made at different times of the year may produce biased samples owing to seasonal migrations or breeding activities

Although no large-scale tagging studies have been performed, field observations and their relatively inefficient and slow swimming speed suggest that *M. glutinosa* are relatively sedentary animals with small home ranges. Among hagfishes, only *Eptatretus burgeri* is known to have seasonal migrations (Fernholm, 1974), and their migration is related to a specific breeding cycle that is unique among hagfishes. *Myxine glutinosa* has no particular breeding period, and adults at all stages of gonadal development are present throughout the year (Walvig, 1963; Martini et al., 1997b). There were no significant differences in the population profiles for animals collected at our primary study site in June–September from one year to the next, and although weather and sea-state conditions prohibited collection in midwinter, no population differences, in terms of size range or abundance, were apparent in ROV surveys performed in December–January as compared to July–August (Martini, personal obs.).

Collections made at different depths may yield different sex ratios and population profiles

The reported depth range of *M. glutinosa* is extensive (50–1100 m). There are no reports of depth stratification by size or sex for any species of *Myxine*, and only suggestions of unequal depth distribution (by size and sex) for two species of *Eptatretus* (*E. stouti* and *E. deani*) (Johnson, 1994; Wakefield, 1990). All known *M. glutinosa* populations have sex ratios that are highly skewed in favor of females, but above the size at sexual maturity there are males and females of all sizes. Any variations in the sex ratios would not affect the morphological parameters we compared because no sexual dimorphism has been reported for these characters in *M. glutinosa* or any other hagfish species.

The IGM data were collected from fresh, rather than preserved, specimens

Fixation shrinkage of 10–15% may occur in preserved specimens (Wisner[1]). This shrinkage would not affect parameters such as cusp counts or slime pore counts, but it would potentially affect total length. Shrinkage alone, however, could not account for the magnitude of the observed differences in maximum total length (950 mm for IGM, versus a maximum of

510 mm elsewhere in the WNA, and 450 mm in the ENA) or the minimum size at sexual maturity (400 mm for the IGM vs. 200 mm for the ENA). Shrinkage may have affected some of the proportional comparisons between the IGM and ENA samples, but the effect is not straightforward. The IGM hagfish (fresh measurement) have proportionately shorter prebranchial segments and tails than the ENA specimens (preserved measurement), and the IGM specimens are more slender (both in width and depth).

The morphological measurements were made by different groups

We do not believe that the differences observed among these populations reflect variation in protocol between the research groups because differences in slime pore counts and cusp counts among the sampled populations remain if the IGM data are set aside, and a single team (Wisner and McMillan) collected the NWA, OGM, ENA, and MAC data sets.

Conclusions

Our analyses of the available data do not support a clean division between eastern and western North Atlantic populations of *M. glutinosa*. We therefore support retention of the species name *M. glutinosa* for both eastern and western populations pending the results of mtDNA analysis or other molecular comparisons.

Specific arguments against species or subspecies division include the following: 1) Considerable variability exists in the total slime pore count among the WNA groups examined; 2) Although there were significant regional differences in slime pore count between the IGM and ENA samples, when compared as absolute values or as percentages of the total slime pore count, this was not the case for the other WNA groups; 3) Total cusp counts were also variable, with significant differences noted between NWA-IGM, NWA-MAC, IGM-ENA, and MAC-ENA; and 4) The degree of differentiation versus the ENA group, in increasing order, would be NWA (trunk slime pore percentage) → OGM (total slime pore count) → MAC (trunk slime pore count and cusp count) → IGM (total, trunk, and tail slime pore counts and cusp count).

This pattern suggests, but does not prove, the existence of clinal variations that may reflect the degree of relative isolation of the populations. Although on a map the Gulf of Maine appears continuous with the western North Atlantic, in fact it is almost completely isolated from the offshore waters by extensive banks and shoals (Fig. 1A). There is only one deepwater connection (260–270 m) between the Gulf of Maine and the North Atlantic. This narrow connection, the Northeast Channel, extends between Brown's Bank (BB), where the majority of the OGM samples were collected, and a shallow ridge that extends northeast from George's Bank (GB). Oceanographically the Gulf of Maine resembles a landlocked sea, like the Mediterranean, rather than a contiguous portion of the North Atlantic. For example, the salinity, temperature, tides, and current dynamics of the Gulf of Maine are distinct from those of the North Atlantic. This combination of factors could isolate hagfish populations within the Gulf of Maine from those elsewhere in the western North Atlantic. The distinct characteristics of the Gulf of Maine environment may also be linked to physiological differences between *M. glutinosa* in the Gulf of Maine versus the eastern North Atlantic. For example, *M. glutinosa* in the eastern North Atlantic have been maintained at water temperatures as high as 15°C (Palmgren, 1927; Gustafson, 1935), whereas specimens at the Shoals Marine Laboratory (Gulf of Maine) quickly become moribund as temperatures approach 10°C (Martini, personal obs.).

The size difference between the IGM and other sampled populations could be a function of age, with members of the IGM population having longer lifespans. However, this is impossible to evaluate without growth rate or longevity data—which does not presently exist for this or any other species of hagfish. Alternatively, the large total size and large size at maturity for hagfish within the Gulf of Maine may reflect the relative availability of food. It is interesting to note that Kendall described winter flounder (*Pleuronectes americanus* [formerly *Pseudopleuronectes americanus*]) of the George's Bank region as a separate species from those found elsewhere in the western North Atlantic, on the basis of its unusually large size; this proposal was ultimately rejected because there were no other morphological differences. It is not clear, however, that the ecosystem in the inner Gulf of Maine is significantly more productive than that of the Skaggerack in the eastern North Atlantic; both areas support substantial commercial fisheries.

Wisner and McMillan (1995) proposed species separation based on maximum size, size at maturity, and differences in the color of preserved specimens. As indicated above, the large maximum size and large size at maturity appear to be characteristic of the IGM population only, rather than a general characteristic of WNA populations of *Myxine*. We remain unable to evaluate the significance of the color differences in preserved specimens noted by Wisner and McMillan (1995) for eastern versus western North

Atlantic *Myxine*. The patterns they described as typical for the WNA are not found in our preserved specimens from the IGM. Further, our field data, which included ROV and submersible observations and trap collections, indicate that the described color patterns are not characteristic of living members of the inner Gulf of Maine populations. Whether they are characteristic of other WNA populations, or typical of only a few subpopulations, remains to be determined.

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Low levels of genetic diversity in highly exploited populations of Alaskan Tanner crabs, *Chionoecetes bairdi*, and Alaskan and Atlantic snow crabs, *C. opilio**

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Abstract.—We used allozyme analyses to investigate genetic variation among commercially exploited populations of *Chionoecetes bairdi* (Tanner) and *C. opilio* (snow) crabs in Alaskan waters. Data were collected from 34 presumptive loci in 1002 *C. bairdi* and 539 *C. opilio* sampled throughout the commercially important range of each species in Alaska. Average observed heterozygosities were 0.027 for *C. bairdi* and 0.013 for *C. opilio*. Low levels of geographic differentiation were detected among populations of *C. bairdi* and *C. opilio*, and our data suggest that subpopulations of *C. bairdi* exist within the Bering Sea. Further, evidence of gene introgression was found between *C. bairdi* and *C. opilio* in the Bering Sea. We also included a geographic isolate, North Atlantic *C. opilio*, in the analyses. Little differentiation was found, and no private alleles were detected in North Atlantic *C. opilio* despite significant geographic separation from Alaskan *C. opilio*.

Five species of the genus *Chionoecetes*, Majidae, are described from the North Pacific region (Rathbun, 1925; Garth, 1958). The nearly circumpolar range of *C. opilio* (snow crab) includes the Bering Sea, the Arctic Ocean, the western North Pacific coast of Asia, and the northern Atlantic Ocean. *Chionoecetes bairdi*, *C. angulatus*, and *C. tanneri* are widespread in the eastern North Pacific (Garth, 1958). *Chionoecetes japonicus* is found only in the western North Pacific along the coast of Asia. In the Alaskan waters of the Bering Sea, the distribution of *C. bairdi* is strongly associated with the continental slope areas along the coast of the Alaska Peninsula, and the Pribilof Islands (Otto, 1982), and there is considerable overlap in the distribution of *C. bairdi* and *C. opilio* (Karinen, 1974).

Commercial fisheries for male *C. bairdi* and *C. opilio* in Alaska, along with king crabs (*Paralithodes* and *Lithodes*) have long been the world's most abundant sources of crabs and have considerable current and historical commercial importance in Alaska (Otto, 1990). *Chionoecetes bairdi* are faster growing, larger, and more valuable than *C. opilio*. Commercial harvests of *C. bairdi* in the Bering Sea and Gulf of Alaska fisheries peaked in the late 1970s, declined throughout the 1980s, and although some populations of *C. bairdi* have recently rebounded, many fisheries remain closed owing to low abundance (Kruse, 1993). Rapid development of the Bering Sea *C. opilio* fishery coincided with the decline of *C. bairdi* fisheries, and although *C. opilio* have dominated landings of Bering Sea crabs since the mid-1980s, catches have also declined dramatically in recent years (ADF&G, 1994).

Declining abundances of Bering Sea and Gulf of Alaska crab populations have intensified competition for the remaining resources and have lead to re-evaluation of crab fishery management practices. Gen-

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erally when a population or stock is modeled, the assumption is made that the individuals within the population are uniform, but it is important that this assumption be verified (Cobb and Caddy, 1989). In practice, a stock is often defined as 1) a production or management unit about which conclusions can be made without regard for differences within the group and exchanges with other groups, or as 2) biologically, a genetically discrete population (reviewed in Cobb and Caddy, 1989). However, stock identity of decapod populations has been largely ignored or problematic (Cobb and Caddy, 1989; Kruse, 1993).

Existing shellfish management units in Alaska were originally established according to historical fishing grounds of red king crab. Current area lines for *C. bairdi* and *C. opilio* were based on mark-and-recapture data, natural geographic barriers, and areas of stock abundance grouped by major fishing grounds. Although genetic surveys were not conducted on unexploited *Chionoecetes* populations in Alaska, the establishment of a genetic baseline is critical for verifying current fishery management units and for monitoring potential fishery-induced genetic changes. Additionally, the genetics of *C. bairdi* and *C. opilio* populations in the Bering Sea is complicated by the presence of hybrids of these two species. *Chionoecetes bairdi* and *C. opilio* appear to have many similar morphological, physiological, and reproductive features (Watson, 1970; Slizkin, 1990) that allow them to hybridize in areas of range overlap (Karinen and Hoopes, 1971; Somerton, 1981; Hoopes et al.[1]).

Many studies suggest that commercial fishing activities may have significant genetic effects on fish stocks without reducing them to near extinction (for example, see reviews in Allendorf et al., 1987; Thorpe, 1993), and genetic selection against fast growth may result from intense fishing pressure (Kruse, 1993; Stevens et al., 1993); however, these effects can be assessed only if there are comparative baseline data.

In 1990 we began genetic investigations of *C. bairdi* and *C. opilio* populations in Alaska using allozyme electrophoresis. Our objectives were 1) to assess genetic variation in exploited populations of *C. bairdi* and *C. opilio* in Alaska and 2) to determine if significant differentiation exists to warrant re-examination of current management units.

Materials and methods

Population sample collections

Samples of *C. bairdi* and *C. opilio* were obtained between 1989 and 1993 from population assessment trawl and pot survey catches, test fishery pot catches, and dockside commercial pot catches. Crabs caught in pots set in adjacent areas were pooled into a single collection (Table 1). *Chionoecetes bairdi* were collected from sites ranging from Seymour Canal in Southeast Alaska to northwest of the Pribilof Islands in the Bering Sea (Table 1; Fig. 1). *Chionoecetes opilio* were collected from sites in the Bering Sea. In addition, we obtained a collection of *C. opilio* from the North Atlantic for comparison with Bering Sea samples. Eighteen collections of *C. bairdi* and nine collections of *C. opilio* were analyzed in this study.

Table 1

Collection information for *Chionoecetes* specimens.

Location number	Location[1]	Date	*n*
Chionoecetes bairdi			
1[2]	Bristol Bay	Jun 90	50
	Bristol Bay	Jun 91	50
2[2]	Bering Sea and Pribilof Islands	Jul 90	50
	Bering Sea and Pribilof Islands	Apr 91	75
	Bering Sea and Pribilof Islands	Jul 92	30
	Bering Sea and Pribilof Islands	Mar 93	50
	Bering Sea and Pribilof Islands	Jul 93	80
3	Port Moller	Jun 90	42
4	Sand Point and Pavlof Bay	Aug 90	50
5	Kodiak N. Mainland	Feb 90	50
6	Kodiak S. Sitkalidak Strait	Feb 90	50
7	Kamishak Bay	Jun 90	50
8	Montague Strait	Jul 90	50
9	Kachemak Bay	Jun 90	50
10	Prince William Sound	Aug 90	50
11	Sullivan Island	Jul 93	100
12	Seymour Canal	Sep 89	50
	Seymour Canal	Jul 93	75
Chionoecetes opilio			
I[2]	Bering Sea	Apr 91	75
	Bering Sea	Mar 93	50
II[2]	St. Matthew Island	Jul 90–Aug 90	100
	St. Matthew Island	Jul 92–Aug 92	100
III[2]	Pribilof Island	Jul 90	44
	Pribilof Island	Aug 90	50
	Pribilof Island	Jul 92	40
	Pribilof Island	Jun 93–Jul 93	80
	Nova Scotia, North Atlantic	Sep 91	97

[1] Latitude and longitude locations available from authors.
[2] Collections within geographic location pooled for analyses; *C. bairdi* collection sites in the Bering Sea and Pribilof Islands were overlapping.

[1] Hoopes, D. T., J. F. Karinen, and M. J. Pelto. 1970. King and Tanner crab research. International North Pacific Fisheries Commission Annual Rep. 1970:110–120.

Figure 1

Locations of samples of *C. bairdi* and *C. opilio* in Alaska analyzed for genetic variation. Numbers correspond to populations described in Table 1. *C. bairdi* sample locations are labelled 1–12. *C. opilio* sample locations are labelled *I–III*.

Tissues (muscle, gill, hepatopancreas, and heart) were dissected from each individual, placed in a labelled tube, which was chilled on wet ice, capped, and frozen at –15°C (1989–90 collections) or in liquid nitrogen (1991–93 collections). Freezing generally occurred within 20 minutes after dissection but in some cases was as long as 1 hour. Tissues were transported to the laboratory on dry ice or liquid nitrogen and stored at –80°C until analysis. Several locations were sampled in multiple years.

Allozyme electrophoresis

Procedures for horizontal starch gel electrophoresis followed those of Harris and Hopkinson (1976) and Aebersold et al. (1987). Activity reflecting 34 presumed loci were resolved with the following buffers (Table 2): 1) N-(3-aminopropyl)-morpholine, citrate (AC, pH 6.1, 6.9) (Clayton and Tretiak, 1972); 2) Tris, borate, citrate, lithium hydroxide (TBCL, pH 8.7) (Ridgway et al., 1970); 3) Tris, citrate (TC, pH 7.0) (Shaw and Prasad, 1970); 4) Tris, citrate (TC, pH 8.0) (Selander et al., 1971); and 5) Tris, borate, EDTA (TBE, pH 8.5) (Boyer et al., 1963). Gene nomenclature followed Shaklee et al. (1990). Allelic standards were used to compare relative mobilities between species.

Genetic differentiation

We estimated allele frequencies, calculated average observed heterozygosities, and tested conformation of genotype frequencies to Hardy-Weinberg expected frequencies with log-likelihood ratios (modified from Weir, 1990) for each collection (α=0.05, adjusted for multiple tests [Rice, 1989]). Samples of *C. bairdi* collected from the Bering Sea and Pribilof Island areas were pooled because sample sites were overlapping. Interannual heterogeneity of multiple-year collections in Bristol Bay, Bering Sea, St. Matthew Island, Pribilof Islands, and Seymour Canal was tested by using log-likelihood statistics (Sokal and Rohlf, 1995). Multiple-year collections within a site were pooled for further analyses if no significant heterogeneity existed (P<0.01). We estimated degree of population subdivision by using Wright's (1978) nonhierarchical F statistics and a hierarchical log-likelihood analysis. We used FSTAT (version 1.2)(Goudet, 1995) to

Table 2

Allozyme protocols to resolve enzyme coding loci in *Chionoecetes* samples. Enzyme nomenclature follows Shaklee et al. (1990), and locus abbreviations are given. Tissue abbreviations are: (M) muscle, (H) heart, (G) gill, and (P) hepatopancreas. Buffers are described in the text.

Enzyme or protein	Enzyme number	Locus	Tissue	Buffer
Aspartate aminotransferase	2.6.1.1	*AAT-1*, AAT-2**	M	TBE
Aconitate hydratase	4.2.1.3	*AH-2**[2]	M	TC7.0
		*AH-3**	M	TC7.0
Adenosine deaminase	3.5.4.4	*ADA-1*, ADA-3**	G,M,H	TBCL
		*ADA-2**	P	TBCL
Alanine aminotransferase	2.6.1.2	*ALAT**	M	TBCL
Cytochrome-b5[1]	1.8.1.4	*CBYR**	M	TBCL
β-N-Acetylgalactosaminidase	3.2.1.53	*βGALA**	G,P	TBCL, TBE
Glyceraldehyde-3-phosphate dehydrogenase	1.2.1.12	*GAPDH**	M	AC6.1
N-Acetyl-β-glucosaminidase	3.2.1.30	*βGLUA**	G,P	TBCL
Glycerol-3-phosphate dehydrogenase	1.1.1.8	*G3PDH-1**	M	TC7.0
		*G3PDH-2**	H,M	TC7.0
Glucose-6-phosphate isomerase	5.3.1.9	*GPI-A1**	M	TBCL
Isocitrate dehydrogenase (NADP+)	1.1.1.42	*IDHP-1**	H	TC7.0
Malate dehydrogenase	1.1.1.37	*MDH-A1*, MDH-A2**	M	AC6.1
Malic enzyme (NADP+)	1.1.1.40	*MEP-1**	H	TC7.0
Mannose-6-phosphate isomerase	5.3.1.8	*MPI**	M	TBE
Dipeptidase	3.4.-.-	*PEPA**	H,P	TBE
Proline dipeptiase	3.4.13.9	*PEPD-2**	G,P	TBCL
Phosphogluconate dehydrogenase	1.1.1.44	*PGDH**	H	TC7.0
Phosphoglucomutase	5.4.2.2	*PGM-1**	M,H	TC7.0
General (unidentified) protein		*PROT-1*, PROT-2*, PROT-3**	M	TBCL
Superoxide dismutase	1.15.1.1	*SOD-1**[2]	M	TBCL
Triose-phosphate isomerase	5.3.1.1	*TPI-1**	M	TBE

[1] This locus expressed with both CBYR* and GR*; preferential stain is CBYR*.
[2] Used in *C. opilio* statistical analysis only.

test significance of F_{ST} values (2000 permutations). Allele frequencies were used to generate distance matrices of Cavalli-Sforza and Edwards chord distances (Cavalli-Sforza and Edwards, 1967). Computations were made with *S-Plus* analytical software (MathSoft Inc., 1997).

Results

Chionoecetes bairdi

Twenty-seven loci were scored consistently in *C. bairdi* populations and were used in the data analyses. Temporal variation was examined for multiple-year collections of *C. bairdi* from Bristol Bay, the Bering Sea and Pribilof Islands area, and Seymour Canal (Table 1). No significant interannual differences ($P<0.01$) were found within each geographic location; therefore these collections were pooled for subsequent analyses.

Fifteen loci, *AAT-1**, *AAT-2**, *AH-3**, *ALAT**, *CBYR**, *G3PDH-1**, *G3PDH-2**, *GPI-A1**, *IDHP-1**, *MDH-A1**, *PEPA**, *PGDH**, *PGM-1**, *PROT-3**, and *TPI-1** were polymorphic (Table 3). At four loci, *G3PDH-1**, *GPI-A1**, *IDHP-1**, and *PEPA**, the most common allele had a frequency of ≤0.95 in at least one population. Twelve monomorphic loci, *ADA-1**, *ADA-2**, *ADA-3**, *βGALA**, *GAPDH**, *βGLUA**, *MDH-A2**, *MEP-1**, *MPI**, *PEPD-2**, *PROT-1**, and *PROT-2** were included in the 27-locus analyses. Seven monomorphic loci, *AH-2**, *mMDH-1**, *PEPD-1**, *SOD-1**, *SOD-2**, *TPI-2**, and *XO** were not scorable in all populations and were not included in our analyses. We could not interpret the genetic basis for the variation we observed in two consistently resolved zones of esterase activity; therefore those data were excluded.

Three collections of *C. bairdi*, Sand Point and Pavlof, Port Moller, and Prince William Sound, with sample sizes of <25 at informative loci, *AH-3** and *IDHP-1**, were not included in the population data analyses; however, we report allele frequencies in Table 3.

Genotype frequencies at all loci conformed to Hardy-Weinberg expectations; therefore we assumed all sam-

Table 3

Allele frequency estimates for *Chionoecetes bairdi* and *C. opilio* collections. ND indicates no data. Dashed lines indicate frequency of 0.000.

	*AAT-1**					*AAT-2**				*AH-2**			
Population[1]	*n*	*100	*64	*210	*120	*n*	*100	*131	*69	*n*	*100	*110	*83
Chionoecetes bairdi													
Bristol Bay pooled	100	0.995	—	—	0.005	100	1.000	—	—	ND			
Bering Sea pooled	283	1.000	—	—	—	274	0.998	—	0.002	280	1.000	—	—
Port Moller 1990	42	1.000	—	—	—	42	1.000	—	—	42	1.000	—	—
Sand Pt/Pavlof 1990	37	1.000	—	—	—	47	1.000	—	—	ND			
Kodiak N. 1990	48	1.000	—	—	—	48	0.990	0.010	—	38	1.000	—	—
Kodiak S. 1990	43	0.988	—	—	0.012	43	0.988	0.012	—	36	1.000	—	—
Kamishak 1990	50	0.990	0.010	—	—	50	1.000	—	—	50	1.000	—	—
Montague St. 1990	42	1.000	—	—	—	49	1.000	—	—	50	1.000	—	—
Kachemak Bay 1990	50	1.000	—	—	—	50	0.990	0.010	—	50	1.000	—	—
Prince Wm. Sd. 1990	50	1.000	—	—	—	50	1.000	—	—	50	1.000	—	—
Sullivan Is. 1993	100	1.000	—	—	—	100	0.995	0.005	—	100	1.000	—	—
Seymour C. pooled	125	1.000	—	—	—	123	1.000	—	—	125	1.000	—	—
Chionoecetes opilio													
Bering Sea pooled	124	0.992	—	0.004	0.004	123	1.000	—	—	115	0.991	0.009	—
St. Matt. Is. pooled	192	0.992	—	—	0.008	193	0.987	0.005	0.008	200	1.000	—	—
Pribilof Is. pooled	211	0.991	0.005	—	0.005	193	0.995	0.003	0.003	214	0.993	0.002	0.005
Atlantic O. 1991	97	1.000	—	—	—	97	0.995	0.005	—	97	1.000	—	—

	*AH-3**					*ALAT**			*CBYR**			*G3PDH-1**			*G3PDH-2*[2]			
Population[1]	*n*	*100	*94	*91	*106	*n*	*100	*87	*n*	*100	*117	*n*	*100	*117	*n*	*100	*86	*111
Chionoecetes bairdi																		
Bristol Bay pooled	100	0.005	0.995	—	—	100	1.000	—	100	1.000	—	96	0.974	0.026	100	1.000	—	—
Bering Sea pooled	279	0.014	0.982	0.004	—	283	0.998	0.002	285	0.998	0.002	265	0.958	0.042	196	0.949	0.008	0.043
Port Moller 1990	42	—	1.000	—	—	42	1.000	—	42	1.000	—	41	0.976	0.024	20	0.950	0.025	0.025
Sand Pt/Pavlof 1990	3	—	1.000	—	—	ND			50	1.000	—	1	1.000	—	ND			
Kodiak N. 1990	38	0.013	0.987	—	—	50	1.000	—	50	1.000	—	46	0.967	0.033	50	0.990	—	0.010
Kodiak S. 1990	33	0.015	0.985	—	—	50	1.000	—	50	1.000	—	37	0.946	0.054	42	1.000	—	—
Kamishak 1990	50	—	1.000	—	—	50	1.000	—	50	1.000	—	49	0.990	0.010	50	1.000	—	—
Montague St. 1990	49	—	1.000	—	—	49	1.000	—	50	1.000	—	50	0.970	0.030	31	1.000	—	—
Kachemak Bay 1990	50	—	1.000	—	—	50	1.000	—	50	1.000	—	50	0.950	0.050	50	0.970	—	0.030
Prince Wm. Sd. 1990	50	—	0.990	0.010	—	50	1.000	—	50	1.000	—	50	0.970	0.030	47	1.000	—	—
Sullivan Is. 1993	95	0.011	0.979	0.011	—	97	1.000	—	50	1.000	—	89	0.933	0.067	49	0.980	—	0.020
Seymour C. pooled	122	0.004	0.992	0.004	—	125	1.000	—	100	1.000	—	122	0.959	0.041	109	1.000	—	—
Chionoecetes opilio																		
Bering Sea pooled	124	0.923	0.077	—	—	123	1.000	—	125	0.996	0.004	125	0.988	0.012	96	0.995	—	0.005
St. Matt. Is. pooled	197	0.939	0.058	—	0.003	195	1.000	—	200	1.000	—	198	0.990	0.010	174	0.994	—	0.006
Pribilof Is. pooled	213	0.937	0.063	—	—	214	1.000	—	214	1.000	—	214	0.998	0.002	183	0.992	0.003	0.005
Atlantic O. 1991	95	0.937	0.063	—	—	97	1.000	—	97	1.000	—	97	1.000	—	94	1.000	—	—

continued

ples were from single panmictic populations. Average observed heterozygosities ranged from 0.016 to 0.035.

Among-population variation

Various measures indicated a low level of population differentiation. F_{ST} values were low, however two loci, *G3PDH-2** and *PEPA** with respective F_{ST} values of 0.0137 (P=0.0005) and 0.0154 (P=0.0020), and the overall F_{ST} value of 0.0046 for 15 polymorphic loci (P=0.0295) differed significantly from zero. A comparison of all *C. bairdi* populations with a hierarchical log-likelihood analysis, indicated significant heterogeneity at four loci, *G3PDH-2**, *IDHP-1**, *PEPA**, and PROT-3*; however the overall statistic was not significant (Table 4). In contrast, when populations

Table 3 (continued)

Population[1]	*GPI-A1**								*IDHP-1**					*MDH-A1**				
	n	*100	*142	*60	*158	*9	*55	*19	*n*	*100	*81	*119	*90	*n*	*100	*79	*128	
Chionoecetes bairdi																		
Bristol Bay pooled	100	0.970	—	0.020	—	0.005	—	0.005	79	0.633	0.278	0.082	0.006	100	1.000	—	—	
Bering Sea pooled	283	0.971	0.005	0.018	—	0.002	0.002	0.002	275	0.562	0.358	0.074	0.006	283	0.995	0.005	—	
Port Moller 1990	42	0.988	—	0.012	—	—	—	—	9	0.611	0.389	—	—	42	1.000	—	—	
Sand Pt/Pavlof 1990	50	0.980	—	0.010	—	0.010	—	—	34	0.691	0.162	0.147	—	8	1.000	—	—	
Kodiak N. 1990	49	0.959	0.010	0.031	—	—	—	—	49	0.592	0.357	0.051	—	49	1.000	—	—	
Kodiak S. 1990	50	0.930	0.020	0.030	—	0.010	—	0.010	36	0.722	0.264	0.014	—	39	1.000	—	—	
Kamishak 1990	50	0.990	—	—	—	0.010	—	—	30	0.683	0.267	0.050	—	50	1.000	—	—	
Montague St. 1990	50	1.000	—	—	—	—	—	—	50	0.510	0.430	0.060	—	50	1.000	—	—	
Kachemak Bay 1990	50	0.980	—	0.010	—	0.010	—	—	28	0.571	0.286	0.107	0.036	50	1.000	—	—	
Prince Wm. Sd. 1990	49	0.990	—	—	—	0.010	—	—	7	0.643	0.214	0.143	—	50	1.000	—	—	
Sullivan Is. 1993	100	0.985	—	0.015	—	—	—	—	82	0.634	0.341	0.024	—	99	1.000	—	—	
Seymour C. pooled	124	0.992	—	0.004	—	0.004	—	—	122	0.574	0.348	0.078	—	125	0.996	—	0.004	
Chionoecetes opilio																		
Bering Sea pooled	125	0.984	0.004	0.004	0.004	—	0.004	—	125	1.000	—	—	—	125	0.992	0.008	—	
St. Matt. Is. pooled	200	0.988	0.013	—	—	—	—	—	196	1.000	—	—	—	200	0.973	0.027	—	
Pribilof Is. pooled	214	0.986	0.012	0.002	—	—	—	—	207	0.990	0.005	0.005	—	213	0.986	0.014	—	
Atlantic O. 1991	97	0.974	0.026	—	—	—	—	—	97	1.000	—	—	—	97	0.990	0.010	—	

Population[1]	*MDH-A2**			*PEPA**				*PGDH**					*PGM-1**						
	n	*100	*65	*n*	*100	*138	*64	*n*	*100	*112	*124	*91	*n*	*100	*82	*114	*103	*88	*75
Chionoecetes bairdi																			
Bristol Bay pooled	100	1.000	—	92	0.940	0.022	0.038	92	0.995	0.005	—	—	100	0.995	—	—	0.005	—	—
Bering Sea pooled	283	1.000	—	279	0.991	0.004	0.005	269	0.996	—	0.004	—	268	0.996	0.004	—	—	—	—
Port Moller 1990	42	1.000	—	39	0.987	—	0.013	18	1.000	—	—	—	42	1.000	—	—	—	—	—
Sand Pt/Pavlof 1990	8	1.000	—	40	0.975	—	0.025	47	1.000	—	—	—	13	1.000	—	—	—	—	—
Kodiak N. 1990	49	1.000	—	48	0.990	0.010	—	40	1.000	—	—	—	47	0.989	—	—	—	—	0.011
Kodiak S. 1990	40	1.000	—	43	0.977	0.012	0.012	34	1.000	—	—	—	38	0.987	0.013	—	—	—	—
Kamishak 1990	50	1.000	—	49	1.000	—	—	45	1.000	—	—	—	50	0.980	0.010	—	—	—	0.010
Montague St. 1990	50	1.000	—	50	1.000	—	—	49	1.000	—	—	—	42	1.000	—	—	—	—	—
Kachemak Bay 1990	50	1.000	—	50	1.000	—	—	46	0.989	—	—	0.011	50	1.000	—	—	—	—	—
Prince Wm. Sd. 1990	50	1.000	—	47	0.989	—	0.011	49	1.000	—	—	—	50	1.000	—	—	—	—	—
Sullivan Is. 1993	99	1.000	—	92	0.995	—	0.005	84	0.994	—	0.006	—	99	0.995	0.005	—	—	—	—
Seymour C. pooled	125	1.000	—	118	0.983	0.004	0.013	119	0.992	—	0.008	—	125	0.992	—	—	—	0.008	—
C. opilio																			
Bering Sea pooled	125	1.000	—	125	0.992	0.008	—	123	0.980	—	0.020	—	125	0.992	0.008	—	—	—	—
St. Matt. Is. pooled	200	0.998	0.002	187	1.000	—	—	183	0.970	—	0.030	—	198	0.982	0.005	0.003	0.003	0.008	—
Pribilof Is. pooled	214	1.000	—	199	0.997	0.003	—	196	0.967	0.008	0.025	—	214	0.993	0.002	—	—	0.005	—
Atlantic O. 1991	97	1.000	—	97	0.995	0.005	—	97	0.985	0.005	0.010	—	97	0.964	—	—	—	0.036	—

Population[1]	*PROT-3**			*SOD-1**			*TPI-1**			
	n	*100	*88	*n*	*100	*109	*n*	*-100	*100	*-41
Chionoecetes bairdi										
Bristol Bay pooled	100	0.010	0.990	125	1.000	—	100	1.000	—	—
Bering Sea pooled	283	0.016	0.984	273	1.000	—	284	0.996	—	0.004
Port Moller 1990	42	—	1.000	39	1.000	—	42	1.000	—	—
Sand Pt/Pavlof 1990	50	—	1.000	50	1.000	—	47	0.979	—	0.021
Kodiak N. 1990	50	—	1.000	50	1.000	—	50	0.990	—	0.010
Kodiak S. 1990	50	—	1.000	50	1.000	—	47	1.000	—	—
Kamishak 1990	50	—	1.000	50	1.000	—	49	1.000	—	—
Montague St. 1990	50	—	1.000	50	1.000	—	50	1.000	—	—

continued

Table 3 (continued)

Population[1]	*PROT-3**			*SOD-1**			*TPI-1**			
	n	*100	*88	*n*	*100	*109	*n*	*-100	*100	*-41
Chionoecetes bairdi, continued										
Kachemak Bay 1990	50	—	1.000	50	1.000	—	50	1.000	—	—
Prince Wm. Sd. 1990	50	—	1.000	50	1.000	—	50	1.000	—	—
Sullivan Is. 1993	100	—	1.000	ND			100	1.000	—	—
Seymour C. pooled	125	—	1.000	125	1.000	—	125	1.000	—	—
Chionoecetes opilio										
Bering Sea pooled	124	0.992	0.008	122	1.000	—	125	0.992	0.004	0.004
St. Matt. Is. pooled	196	0.997	0.003	198	0.997	0.003	198	0.995	0.002	0.002
Pribilof Is. pooled	214	0.986	0.014	211	0.998	0.002	214	1.000	—	—
Atlantic O. 1991	97	1.000	—	97	1.000	—	97	0.990	0.010	—

[1] Port Moller, Sand Point/Pavlof Bay, and Prince William Sound *C. bairdi* populations not included in analyses.
[2] *G3PDH-1*87* was pooled with **100*.

were grouped by major geographic regions (Bering Sea, Gulf of Alaska, and Southeast Alaska) for comparison, the overall log-likelihood statistic was highly significant ($P<0.01$, Table 4). *G3PDH-2** and *PROT-3** contributed most to the observed among-region heterogeneity. Within the Bering Sea, pooled samples collected from Bristol Bay (east of approximately 162°45'W long.) were significantly different from pooled samples from the Bering Sea and Pribilof Island areas (west of approximately 167°00'W long.). In this comparison, *G3PDH-2**, *IDHP-1**, and *PEPA** allelic frequencies differed significantly.

The following were the low-frequency alleles detected according to their respective major geographic regions: 1) Bering Sea, *AAT-2*69*, *ALAT*87*, *CBYR*117*, *G3PDH-2*86*, *GPI-A1*55*, *MDH-A1*79*, *PGDH*112*, *PGM-1*103*, and *PROT-3*100*; 2) Gulf of Alaska, *AAT-1*64*, *PGDH*91*, and *PGM-1*75*; and 3) Southeast Alaska, *MDH-A1*128* and *PGM-1*88*. The *PROT-3*100* allele, likely an introgressed *C. opilio* allele, contributed significantly to the overall heterogeneity observed among the major geographic regions of Bering Sea, Gulf of Alaska, and Southeast Alaska. Genetic distance measurements (Cavalli-Sforza and Edwards, 1967) within *C. bairdi* populations ranged from 0.031 to 0.059.

Chionoecetes opilio

Twenty-nine loci were scored consistently in all collections and were used in the data analyses. No significant temporal variation ($P<0.01$) was found within multiple-year collections in the Bering Sea, St. Matthew Island, and the Pribilof Islands. We pooled these collections for further analyses.

Seventeen loci, *AAT-1**, *AAT-2**, *AH-2**, *AH-3**, *CBYR**, *G3PDH-1**, *G3PDH-2**, *GPI-A1**, *IDHP-1**, *MDH-A1**, *MDH-A2**, *PEPA**, *PGDH**, *PGM-1**, *PROT-3**, *SOD-1**, and *TPI-1**, were polymorphic in at least one population (Table 3). Twelve monomorphic loci were *ADA-1**, *ADA-2**, *ADA-3**, *ALAT**, *βGALA**, *GAPDH**, *βGLUA**, *MEP-1**, *MPI**, *PEPD-2**, *PROT-1**, and *PROT-2**. One polymorphic locus, *AH-3**, was variable at a frequency of ≥0.05 in at least one population.

Genotype frequencies at all loci conformed to Hardy-Weinberg expectations; therefore we assumed all samples were from single panmictic populations. Average observed heterozygosities were lower than those for *C. bairdi* and ranged from 0.012 to 0.013 in Alaskan populations; the average heterozygosity was 0.010 in Atlantic Ocean *C. opilio*.

Among-population variation

F_{ST} of 17 polymorphic loci was not significantly different from zero for Alaskan populations ($P=0.4270$) or when the Atlantic Ocean collection was included ($P=0.7130$). However, the F_{ST} value for *PGM-1** was highly significant ($P=0.0050$) in comparisons of Atlantic Ocean and Alaskan *C. opilio*. A hierarchical log-likelihood analysis of these loci revealed very low levels of heterogeneity among all *C. opilio* (Table 5). In this analysis, *PGM-1** was also highly significant ($P=0.0071$) in comparisons of Atlantic Ocean and Alaskan *C. opilio*. Among all *C. opilio*, *PGM-1** was significant ($P=0.0361$). The overall log-likelihood statistic for all loci among all *C. opilio* was significant ($P=0.0382$)(Table 5). Low-frequency alleles detected in Alaskan collections were *AAT-1*64*, **210*, and **120*, *AAT-2*69*, *AH-2*110* and **83*, *AH-3*106*, *CBYR*117*, *G3PDH-1*117*, *G3PDH-2*86* and **111*, *GPI-A1*60*,

*158, and *55, IDHP-1*81 and *119, MDH-A2*65, PGM-1*82, *114, and *103, PROT-3*88, SOD-1*109, and TPI-1*-41. Differing PGM-1* alleles and allele frequencies contributed most to the overall levels of differentiation observed between Alaskan and Atlantic Ocean *C. opilio* populations. Multilocus between-population chord distance measures ranged from 0.029 to 0.033 in Alaskan collections and increased to 0.043 when we added the Atlantic Ocean population.

Comparison of *C. bairdi* and *C. opilio* from Alaska

A total of 27 loci, *AAT-1*, AAT-2*, AH-3*, ADA-1*, ADA-

Table 4

Hierarchical log-likelihood analysis for *Chionoecetes bairdi*.

	df	*AAT-1**	df	*AAT-2**	df	*AH-3**	df	*ALAT**
Total	16	13.10	16	12.70	16	14.72	8	2.21
Among	2	1.23	2	6.35*	2	1.90	1	1.60
Within	14	11.87	14	6.35	14	12.82	7	0.61
Bering Sea	2	2.69	2	0.62	2	2.54	1	0.61
Gulf of Alaska	12	9.18	12	5.73	12	10.28	6	0.00
Among	2	1.49	2	0.10	2	1.54	1	0.00
Within	10	7.69	10	5.63	10	8.74	5	0.00
Northern Gulf	8	7.69	8	4.83	8	5.38	4	0.00
Southeast	2	0.00	2	0.80	2	3.36	1	0.00
	df	*CBYR**	df	*G3PDH-1**	df	*G3PDH-2**	df	*GPI-A1**
Total	8	2.21	8	8.25	16	43.07**	40	37.66
Among	1	1.61	1	0.31	2	13.82**	5	3.89
Within	7	0.60	7	7.94	14	29.25**	35	33.77
Bering Sea	1	0.60	1	1.01	2	16.84**	5	3.50
Gulf of Alaska	6	0.00	6	6.93	12	12.41	30	30.27
Among	1	0.00	1	1.16	2	0.49	5	6.25
Within	5	0.00	5	5.77	10	11.92	25	24.02
Northern Gulf	4	0.00	4	3.85	8	9.94	20	21.57
Southeast	1	0.00	1	1.92	2	1.98	5	2.45
	df	*IDHP-1**	df	*MDH-A1**	df	*PEPA**	df	*PGDH**
Total	24	38.63*	16	10.40	16	30.30*	24	15.60
Among	3	3.79	2	5.96	2	4.55	3	2.87
Within	21	34.84*	14	4.44	14	25.75*	21	12.73
Bering Sea	3	3.56	2	1.82	2	14.04	3	3.91
Gulf of Alaska	18	31.28	12	2.62	12	11.71	18	8.82
Among	3	5.51	2	0.78	2	2.62	3	0.77
Within	15	25.77	10	1.84	10	9.09	15	8.05
Northern Gulf	12	20.83	8	1.84	8	8.22	12	7.13
Southeast	3	4.94	2	0.00	2	0.87	3	0.92
	df	*PGM-1**	df	*PROT-3**	df	*TPI-1**	df	Overall
Total	32	27.40	8	18.22*	8	6.29	256	280.75
Among	4	6.43	1	17.83**	1	0.58	32	72.71**
Within	28	20.97	7	0.39	7	5.71	224	208.04
Bering Sea	4	3.87	1	0.39	1	1.21	32	57.22
Gulf of Alaska	24	17.10	6	0.00	6	4.50	192	150.82
Among	4	3.01	1	0.00	1	0.77	32	24.49
Within	20	14.09	5	0.00	5	3.73	160	126.33
Northern Gulf	16	13.38	4	0.00	4	3.73	128	108.40
Southeast	4	0.71	1	0.00	1	0.00	32	17.93

* Test is significant at $\alpha = 0.05$.
** Test is significant at $\alpha = 0.01$.

2, ADA-3*, ALAT*, CBYR*, βGALA*, GAPDH*, βGLUA*, G3PDH-1*, G3PDH-2*, GPI-A1*, IDHP-1*, MDH-A1*, MDH-A2*, MEP-1*, MPI*, PEPA*, PEPD-2*, PGDH*, PGM-1*, PROT-1*, PROT-2*, PROT-3**, and *TPI-1**, were scored in all *C. bairdi* and *C. opilio* populations analyzed; 16 loci, *AAT-1*, AAT-2*, AH-3*, ALAT*, CBYR*, G3PDH-1*, G3PDH-2*, GPI-A1*, IDHP-1*, MDH-A1*, MDH-A2*, PEPA*, PGDH*, PGM-1*, PROT-3**, and *TPI-1**, were polymorphic in at least one population of either species. Eleven loci, *ADA-1*, ADA-2*, ADA-3*, βGALA*, GAPDH*, βGLUA*, MEP-1*, MPI*, PEPD-2*, PROT-1**, and *PROT-2**, were monomorphic for the identical allele. Significant differences ($P<0.01$) between the two species were detected at eight loci, *AH-3*, G3PDH-1*, GPI-A1*, IDHP-1*, MDH-A1*, PEPA*, PGDH**, and *PROT-3**. Two loci, *AH-3** and *PROT-3**, were particularly informative with nearly fixed differences for alternate alleles (Table 3). In addition, with the exception of *C. opilio* from the Pribilof Island area collections, *C. opilio* expressed only the *IDHP-1*100* allele, whereas *C. bairdi* were highly variable. Several low-frequency variants ($P<0.05$) also contributed to the overall differences between the species. Numerous low-frequency alleles detected in only Bering Sea collections of *C. bairdi* were also detected in Alaskan *C. opilio* collections, including the following: *AAT-2*69, CBYR*117, G3PDH-2*86, GPI-A1*55, MDH-A1*79, PGM-1*103*, and *PROT-3*88*. Also, a rare allele, *PGDH*112*, was detected only in Bristol Bay *C. bairdi* and in Pribilof Island and Atlantic Ocean *C. opilio*.

Multilocus variation between species was estimated by genetic-distance measures. Between-species genetic-distance measures ranged from 0.222 to 0.251. The largest genetic distance was between Atlantic *C. opilio* and two northern Gulf of Alaska *C. bairdi* populations, those of Kachemak Bay and Montague Strait. The smallest between-species genetic distance was that for Pribilof Island and Bering Sea *C. opilio* compared with that for Bering Sea and Pribilof Island *C. bairdi*.

Table 5

Hierarchical log-likelihood analysis for *Chionoecetes opilio*.

Source	df	Overall
Total	96	121.93*
Among	32	41.63
Within	64	80.30
Bering Sea	64	80.30
Atlantic Ocean	0	0.00

* Significant value ($P<0.05$)

Chiocoetes bairdi × *C. opilio* hybrids

Hybrids between *C. bairdi* and *C. opilio* crabs in the Bering Sea have been identified morphologically and genetically (Karinen and Hoopes, 1971; Johnson, 1976; Grant et al., 1978; Hoopes et al.[1]). Several collections in our study had allele frequencies suggesting either low levels of introgression between the species or the inclusion of hybrid or backcross individuals in the collection. For example, low frequencies of *PROT-3*100* were observed in *C. bairdi* crabs from Bristol Bay, the Bering Sea, and the Pribilof Islands. *PROT-3*100* was not observed in *C. bairdi* from non-Bering Sea collections. Similarly, *PROT-3*88* was observed in *C. opilio* collections from the Bering Sea, St. Matthew Island, and the Pribilof Islands, and low frequencies of *IDHP-1*81* and **119* were observed in Pribilof Island *C. opilio* collections; these alleles were not observed in *C. opilio* collected from the Atlantic Ocean.

Discussion

Allozyme electrophoresis techniques have been used extensively to describe evolutionary relationships within genera of decapod crustaceans (Bert, 1986; Bert and Harrison, 1988; Busack, 1989; Abdullah and Shukor, 1993); however, these techniques have generally revealed very low levels of intraspecific genetic variation (Nelson and Hedgecock, 1980; Smith et al., 1980; Busack, 1988; Seeb et al., 1990b). Exceptions to this generalization are found in species that occur over broad geographic areas or in widely different environments (Nelson and Hedgecock, 1980; Mulley and Latter, 1981; Kartavtsev et al., 1991). Significant population heterogeneity has been found in species that exhibit highly specialized life history attributes (Stevens, 1991) and in some freshwater species (Macaranas et al., 1995; Fetzner et al., 1997). Within a marine species, Seeb et al. (1990a) discriminated populations of red king crab from major geographic areas of the Gulf of Alaska and Bering Sea. Allozyme techniques have also been used to examine seasonal variability of decapod larval, megalopal, and adult allelic frequencies (Kordos and Burton, 1993).

Davidson et al. (1985) examined population structure in North Atlantic *C. opilio* using allozymes and interpreted their observed esterase polymorphisms as phenotypic expressions of probable genotypic differences. However, we feel caution should be used in interpreting their data until genetic transmission of these markers can be shown by inheritance studies because we were unable to interpret the genetic basis of observed esterase activity.

The importance of tissue quality for allozyme studies is well documented (e.g. Utter et al., 1987) but is particularly critical for crustacean tissue, which degrades more rapidly than finfish tissue. Laboratory analysis revealed obvious differences in enzyme resolution for several loci that resulted in conservative allele pooling and loss of some population data. Optimal sample handling may have increased detectable variation.

Population diversity of *C. bairdi*

We detected differences among *C. bairdi* populations of the three major geographic regions: Bering Sea, Gulf of Alaska, and Southeast Alaska. Most notably, we detected population subdivision within the Bering Sea. Samples collected in Bristol Bay (east of approximately 162°45'W long.) were statistically different from samples collected near the Pribilof Islands (west of approximately 167°00'W long.).

Other biological data support our inference that subpopulations of *C. bairdi* occur within the Bering Sea. Using trawl survey data from 1974 onward, Otto (1982) reported size-frequency distributions of *C. bairdi* in the Pribilof Islands that were different from those in the area north of the Alaska Peninsula, including Bristol Bay. Further, as National Marine Fisheries Service (NMFS) trawl assessment surveys expanded westward, it became evident that crabs in the Pribilof area were larger in size compared with those along the continental slope north and west of the Pribilof Islands. Somerton (1981) found size differences among large females from the eastern Bering Sea seemed to partition into two subareas along 167°15'W long. The mean size of adult females was quite constant in the eastern subarea (east of 167°15'W long.) but decreased steadily in the western subarea. Although both investigators speculated upon the possibility of genetic or environmental factors causing these differences, the species has been considered a single Bering Sea stock for management purposes (Otto, 1982). In our study, we lacked *C. bairdi* specimens from west of approximately 173°W long. and thus were unable to test whether crabs collected from near the Pribilof Islands differed from crabs collected near the continental slope. Although there does not appear to be a precise correlation between our findings and the observations of Otto (1982) and Somerton (1981), all data seem to suggest that *C. bairdi* in the Bering Sea may not be composed of a single panmictic population.

However, any conclusions we may draw from biochemical data should be confirmed by other types of data. The American lobster (*Homarus americanus*) is a case in point. Tracey et al. (1975) noted genetic and morphological differences between inshore and offshore populations. In tagging studies, Fogarty et al. (1980) demonstrated limited movement of lobsters released at inshore stations, in contrast with extensive seasonal migrations by lobsters tagged at offshore locations. These studies indicated that despite the potential for genetic exchange during seasonal mixing, the inshore and offshore populations retained their genetic identity.

The planktotrophic larvae of *Chionoecetes* may spend up to two months in surface waters (Slizkin, 1990), raising the possibility that larvae released in one area may become recruits in another. Further, most of what is known or hypothesized about migration of Bering Sea *C. bairdi* is based upon abundance and distribution estimates from annual NMFS trawl surveys and subsequent fishery captures.[2] Migration studies of *Chionoecetes* in Alaska have been hindered by tag losses after molting. Development of a permanent tag for *Chionoecetes* would provide a valuable tool for examining population migration and further for evaluating the null hypothesis of panmixia. Our findings of regional and within-Bering Sea heterogeneity among *C. bairdi* populations merit further investigation.

Population diversity of *C. opilio*

We detected only small differences between Bering Sea and North Atlantic *C. opilio*, primarily in *PGM-1** allele frequencies. The low-frequency alleles of other loci observed in Alaskan *C. opilio* did not contribute significantly to overall differences. Although sampling error may have been a factor (Gregorius, 1980) in detection of rare alleles, no private alleles were found in the North Atlantic. The minimal genetic differentiation among this circumpolar species contrasts with findings in halibut (*Hippoglossus*), herring (*Clupea*) and cod (*Gadus*) (Grant, 1987) where significant differentiation has been described across a similar geographic range. The close genetic affinity of the Bering Sea *C. opilio* collections with the collection from the North Atlantic and the detection of low-frequency Bering Sea *Chionoecetes* alleles in the North Atlantic suggest recent or ongoing gene flow. This possibility is supported by Garth (1958) whose range description includes a distribution of *C. opilio* northward (from the Bering Strait) and eastward through the Beaufort Sea and Davis Strait to the North Atlantic. This species tolerates very low temperatures; the optimum temperature for immature individuals has negative values even in the summer (Slizkin, 1990). Thus, it is plausible to hypoth-

[2] Morrison, R. 1997. Alaska Dep. Fish and Game, P.O. Box 920587, Dutch Harbor, AK 99692. Personal commun.

esize gene flow through these northern seas even in the presence of sea ice pack. Alternatively, it is possible that gene flow is restricted, but that the differentiating forces of drift, selection, and mutation have not yet produced significant detectable genetic divergence.

Species differentiation, hybrids, and gene introgression

The morphological criteria for differentiating *C. bairdi* and *C. opilio* have been well described (Rathbun, 1925; Garth, 1958; Karinen and Hoopes, 1971). However, a few crabs in our study that met one or more morphological criteria were probably hybrid or recombinant individuals. Their composite genotypes were atypical of the parental species and were instead indicative of F_1 hybrids or backcross matings. Species differentiation in allelic frequencies was observed between *C. bairdi* and *C. opilio*, most notably for *AH-3**, *IDHP-1**, and *PROT-3**. The unusual composite genotypes were most clearly differentiated by the *PROT-3*100* allele in *C. bairdi* collections, and conversely, by the *PROT-3*88* allele in the *C. opilio* collections from the Bering Sea. The *PROT-3*100* allele contributed significantly to the among-regional differences in *C. bairdi*. This marker is also very useful for investigation of hybridization between these species.

Gene flow and geographic barriers

Our findings are consistent with previous electrophoretic studies that infer that decapod crustaceans, especially large, mobile species, exhibit low levels of variation at allozyme markers (Nelson and Hedgecock, 1980). The high dispersal potential of marine species is often used to explain the low levels of variation detected among populations (Avise, 1994). Such distribution appears to be the case with *Chionoecetes* as well as with other marine organisms with similar geographic distributions in the North Pacific, Gulf of Alaska, and Bering Sea, such as Pacific halibut (Grant et al., 1984), Pacific herring (Grant and Utter, 1984), Pacific cod (*Gadus macrocephalus*) (Grant et al., 1987), Pacific ocean perch (*Sebastes alutus*) (Seeb and Gunderson, 1988), and red king crab (*Paralithodes camtschaticus*) (Seeb et al., 1990a).

Limits to the actual dispersal of marine species, despite high dispersal potential, may periodically or continuously limit gene flow in some directions (Avise, 1994 and references therein). The Alaska Peninsula–Aleutian chain appears to be a significant barrier to gene flow in some species, such as Pacific ocean perch (Seeb and Gunderson, 1988), Pacific herring (Grant and Utter, 1984), rock sole (*Pleuronectes bilineatus*) (Mulligan et al., 1995) and red king crab (Seeb et al., 1990a).

The Alaska Peninsula–Aleutian Chain appears to limit gene flow among *C. bairdi* populations as evidenced by the differentiation detected among regions above and below this geographic barrier. The lack of introgressed *C. opilio* alleles in the Gulf of Alaska and Southeast Alaska populations studied also supports this view. Our findings suggest that the numerous rare alleles observed in Bering Sea, and not Atlantic, populations of *Chionoecetes* may be ancient alleles that have been maintained over time in the large populations that have inhabited these waters; however, larger sample sizes of Atlantic Ocean *C. opilio* are needed to confirm this hypothesis. Detection of low-frequency Bering Sea *Chionoecetes* alleles in North Atlantic *C. opilio* and the lower heterozygosity of North Atlantic *C. opilio*, coupled with the lack of congeners in the North Atlantic, allow speculation that the genus *Chionoecetes* may have arisen in the North Pacific.

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Abstract.—Some combinations of trawler, trawl, and crew catch fish better than others. Systematic error enters catch per unit of effort (CPUE) data from trawl surveys through such relative differences in efficiency among sampling instruments. Correcting relative fishing power differences can remove bias due to systematic error but may also increase the variance of the mean CPUE estimate. As a result, the overall error of the estimate may actually become worse, even when the fishing power difference is statistically significant. A decision rule specified by the mean square error (MSE) of the mean CPUE estimate avoids this mistake: namely a correction that reduces the error in the mean CPUE estimate would be applied, a correction that increases the error would not be applied. I describe and demonstrate an algorithm, based on minimizing the MSE, for deciding to correct a fishing power difference. The strategy requires that a probability density function exist that models the CPUE data reasonably well.

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A decision rule based on the mean square error for correcting relative fishing power differences in trawl survey data

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Trawl surveys are often used to collect data on catch observations standardized by fishing effort (the catch per unit of effort [CPUE]), and the mean CPUE is often interpreted as an index of abundance. Ideally, fishing power, or fish catching efficiency, must be held constant in trawl surveys lest altered catch rates be confounded with changes in abundance of fish or invertebrates. Unfortunately, the sampling instrument is a complex system that includes the vessel, vessel operators, and fishing gear, all of which may vary from survey to survey, introducing changes in fishing power (Gulland, 1956). Correcting fishing power differences seems necessary for proper interpretation of mean CPUE. However, methods have not been established for determining if an improved estimate of mean CPUE actually results from such correction.

Relative differences in fishing power make standardization in trawl surveys difficult. Technological changes in fishing gear, as well as replacement of older research vessels, may affect fishing power (Azarowitz, 1981; Byrne et al., 1991). Fishing power differences are an inherent part of multiple vessel surveys. Examples of this type of survey are annual and triennial surveys in several regions of the north Pacific Ocean and Bering Sea conducted by the Alaska Fisheries Science Center (AFSC) of the National Marine Fisheries Service (NMFS) (Harrison, 1992; Weinberg et al., 1994; Munro and Hoff, 1995; Goddard and Zimmermann[1]) and the International Young Fish Survey in the North Sea (Anonymous[2]). Koeller and Smith (1983) reported change in a single vessel's ability to measure speed over a 3-year period and hypothesized that this may have altered its fishing power from year to year. Operator effects have also been shown to account for fishing power differences among vessels (Munro and Hoff, 1995) and thus may be inferred for change in operators of a single vessel. (In what

[1] Goddard, P., and M. Zimmermann. 1993. Distribution, abundance, and biological characteristics of groundfish in the eastern Bering Sea based on results of the U.S. bottom trawl survey during June–September 1991. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., Alaska Fish. Sci. Cent., 7600 Sand Point Way NE, Seattle, WA 98115-0070, Proc. Rep. 93-15, 324 p.

[2] Anonymous. 1986. Manual for the International Young Fish Surveys in the North Sea, Skagerrak, and Kattegat. International Council for the Exploration of the Sea, Palaegade 2-4, DK-1261, Copenhagen K, Denmark. ICES Council Meeting 1986/H:2.

follows, "vessel" refers to the entire system that comprises the sampling instrument, from the bow of the fishing vessel to the codend.)

A fishing power difference forces a choice between two estimators of mean CPUE, one that incorporates a fishing power correction and one that does not. Correcting a fishing power difference amounts to changing an observation to an estimate. The following model is used to estimate what a standard vessel would have caught had it executed exactly the same tow as was done by a nonstandard vessel:

$$\hat{x}_i = y_i \hat{FPC},$$

where $\hat{x}_i$ = estimated CPUE at station i by the standard vessel;
y_i = observed CPUE at station i by the nonstandard vessel; and
$\hat{FPC}$ = estimated fishing power correction factor.

Each original observation, y_i, has no error beyond measurement error. Every $\hat{x}_i$ has error due to the variance of the estimate of FPC. Consequently the mean CPUE estimated from the $\hat{x}_i$ has at least two components of variation, one stemming from the usual sampling variance in the observations (y_i), the other due to uncertainty in the estimate of FPC. This added component of estimation error has been recognized as the cost of correcting systematic error in the observations, but only in passing, (Sissenwine and Bowman, 1978; Byrne et al., 1981; Koeller and Smith, 1983; Fanning, 1984).

Estimators are often chosen on the basis of their relative error, yet most researchers have ignored this in deciding whether or not to correct a fishing power difference. Investigations have been focused on estimating the difference but have not evaluated it in terms of estimating mean CPUE. Very few decision rules have been explicitly stated, most having been implied by testing the statistical significance of the fishing power difference itself. Early CPUE calibrations (Gulland, 1956; Robson, 1966) were based on multiplicative models of different sources of variability in CPUE data, including vessel effects. Log transformation of the data produced linear models with coefficients that could be estimated with regressions and for which classical hypotheses could be formulated and tested. Sissenwine and Bowman (1978), Kimura (1981), and Gavaris (1980) have followed this strategy in their decisions to apply FPCs. Gavaris (1980) estimated the FPC using the method of Bradu and Mundlak (1970) and reported approximate confidence intervals, without explicitly stating a decision rule. Fanning (1984) proposed an explicit decision rule using a beta-distributed index for the fishing power difference in paired observations. If the confidence interval included the value that represented identical fishing power, he recommended that the estimated FPC not be applied. Byrne and Fogarty (1985) tested the significance of fishing power differences using Hotelling's t-squared test when several species were considered simultaneously, or the nonparametric Friedman's test for a single species. They offered no interpretation of a significant fishing power difference, in particular, whether or not it should be corrected. The t-test was used by Byrne et al. (1991) to determine the significance of a fishing power difference. In response to a significant difference, they estimated an FPC using the method of Bradu and Mundlak (1970). They then produced confidence intervals for that estimate using a bootstrap approximation. However, they did not state an explicit decision rule based on those intervals.

Correcting a fishing power difference would be worthwhile only when it reduces the error in the estimate of mean CPUE. Statistical significance of a fishing power difference is not a compelling justification because the cost of the added uncertainty may out weigh the benefit of removing bias that entered through systematic error in CPUE data. If the estimate of a correction factor has a lot of uncertainty, then the error of the estimate of mean CPUE could actually become worse by correcting data, even for a statistically significant fishing power difference. A decision rule for correcting a fishing power difference must avoid this mistake by accounting for the cost of correcting as well as the benefit. Such a rule would permit choosing the estimate of mean CPUE that yields the lower total error.

Methods

The notion of the mean square error (MSE) lends a useful structure for defining such a decision rule. The MSE is a widely recognized measure of error between an estimator and its parameter (Mood et al., 1974). The MSE is defined as

$$MSE\ [\hat{C}] = E\left[(\hat{C} - C)^2\right],$$

which is the expectation of the squared difference between the estimator of mean CPUE, $\hat{C}$, and the parameter being estimated, true CPUE or, C. The MSE can be rewritten as

$$MSE\ [\hat{C}] = \mathrm{Var}[\hat{C}] + b^2[\hat{C}],$$

or the sum of the variance and the squared bias of the estimator. By defining the following estimators,

$\hat{C}(\underline{w})$ = estimator as a function of uncorrected data

$\hat{C}(\hat{\underline{w}}_{\hat{FPC}})$ = estimator as a function of data corrected with an estimated *FPC*,

where $\underline{w} = (x_1, x_2, \ldots, x_{n_x}, y_1, y_2, \ldots y_n)$

= a mixed vector of CPUE observations from two vessels

and

$\underline{w}_{\hat{FPC}} = (x_1, x_2, \ldots, x_{n_x}, y_1 \hat{FPC}, y_2 \hat{FPC}, \ldots y_{n_y} \hat{FPC})$

= a mixed vector of CPUE observations and estimates,

a model for the decision rule can be stated as: Apply the FPC if

$$MSE\left[\hat{C}(\underline{w})\right] > MSE\left[\hat{C}(\hat{\underline{w}}_{\hat{FPC}})\right]$$

and do not apply the FPC if

$$MSE\left[\hat{C}(\underline{w})\right] \leq MSE\left[\hat{C}(\hat{\underline{w}}_{\hat{FPC}})\right].$$

(Note, this explication of the MSE of mean CPUE has been framed in terms of a single survey with two vessels. But the notion of MSE lends itself equally well to any situation in which data must be "corrected," including the common case of a single, nonstandard vessel conducting a standard survey.)

This decision rule is unattainable because it requires that the true value of the fishing power difference and CPUE sampling distributions be known. However, simulations can be used to estimate the mean square error. One such simulation strategy takes the following form: Assume a probability distribution for CPUE. Generate realizations of this distribution to represent a survey in which a fishing power difference is suspected. Impose an assumed fishing power difference on the simulated survey. Estimate the fishing power difference and apply the estimate to correct the assumed fishing power difference. (Estimating the fishing power difference may require further distributional assumptions and simulations, depending on the estimator and the kind of data it requires, especially if fishing power difference is to be estimated from experiments conducted independently of the survey.) The MSEs of the estimated mean CPUE are then calculated from the realizations with and with out the fishing power corrections. This procedure is repeated for a range of selected fishing power differences. Whether the observed fishing power difference (estimated from real data) falls within the range of the fishing power difference for which correcting reduces the MSE of the estimated mean CPUE can then be determined.

This general strategy is illustrated by constructing an algorithm to apply it to a real problem. Any algorithm for implementing this decision rule will depend on specific circumstances. In this case the particulars are defined by a fishing power problem in an annual survey of the eastern Bering Sea, conducted by the AFSC (Wakabayashi et al., 1985; Goddard and Zimmermann[1]). Two vessels systematically sample all strata, following interleaved station patterns that produce approximately equal numbers of CPUE observations. From these two sets of unpaired data a fishing power difference between two vessels is estimated for each of a number of species. The question is "Should this estimated FPC be used to correct CPUEs of one vessel to the fishing efficiency of the other?" This general MSE decision rule takes the following form (the specifics of the Bering Sea survey being addressed within this framework):

1 Simulate surveys from an appropriate sampling distribution for data collected by a "standard" vessel.
2 Impose a known fishing power difference on the CPUE data in each simulated survey. (In these examples half the data were altered to emulate a two-vessel survey.)
3 For each simulated survey, estimate an FPC to correct the fishing power difference that was imposed in the previous step. (FPCs may be estimated from simulation from independent experimental data or, as in these examples, estimated from the simulated survey itself. The important aspect is that the error structure of the FPC estimator be incorporated in the simulation process.)
4 Estimate the mean CPUE for each simulated survey with and without correcting for the fishing power difference.
5 Repeat steps 2 through 4 for a range of fishing power differences.
6 Compute MSEs for estimated mean CPUE for each level of fishing power difference.
7 Plot the estimated MSEs against the fishing power differences imposed in Step 2 (Fig. 1).
8 Determine the range of fishing power difference where the MSE for corrected data is lower than the MSE for uncorrected data (Fig. 1).

The region of increased error is centered around the value 1.0, which represents equal fishing powers, and is sandwiched between regions of reduced error (Fig. 1). The smaller the true fishing power difference the more likely that correcting it will lead to increased error in mean CPUE, and the greater the fishing

power difference the more likely that correcting it will improve error in mean CPUE. For the range of the relative fishing power difference for which correction increases (becomes worse), the MSE will be called the "noncorrection region." The two ranges of the relative fishing power difference for which correcting reduces (improves) the MSE will be referred to collectively as the "correction region."

This procedure has four critical elements: simulating the CPUE data, the estimator of FPC, the estimator of mean CPUE, and the sample size in each simulation. The CPUE data (kilograms per hectare) were simulated with the Δ-distribution. The Δ-distribution has been proposed as an appropriate distribution for data that include the value 0.0 and that are heavily skewed to the right (Pennington, 1983; McConnaughey and Conquest, 1992). The probability density function for the Δ-distribution has parameters p, the probability of an observation with the value 0.0, and μ and σ, the conventional defining parameters of the lognormal distribution, which are the population mean and standard deviation of the log-transformed elements, respectively (Aitchison and Brown, 1957). The parameters for this distribution were calculated with CPUE data for flathead sole (*Hippoglossoides elassodon*) and walleye pollock (*Theragra chalcogramma*) collected in the 1992 eastern Bering Sea survey (Table 1; Fig. 2). These two species were chosen to illustrate cases of moderate and extreme skewness to the right. The mechanism for imposing a fishing power difference is also part of simulating each survey. In these examples the relative difference was applied by multiplying each CPUE from the nonstandard vessel by a ratio that represented the true mean nonstandard CPUE over the true mean standard CPUE. Two-hundred surveys were simulated at each of twenty preselected fishing power differences (Table 2). In each simulated survey, half of the data were selected to represent the standard vessel and the fishing power difference was imposed on the other half of the data, representing the nonstandard vessel. The sample sizes in two of the simulations were based on the number of observations used to calculate the parameters of the Δ-distribution: 149 per vessel for pollock and 144 per vessel for flathead sole. The third simulation was based on 50 observations per vessel for flathead sole. The smaller sample size is similar to the number of tows made in the larger strata of the annual Bering Sea survey (Goddard and Zimmermann[1]).

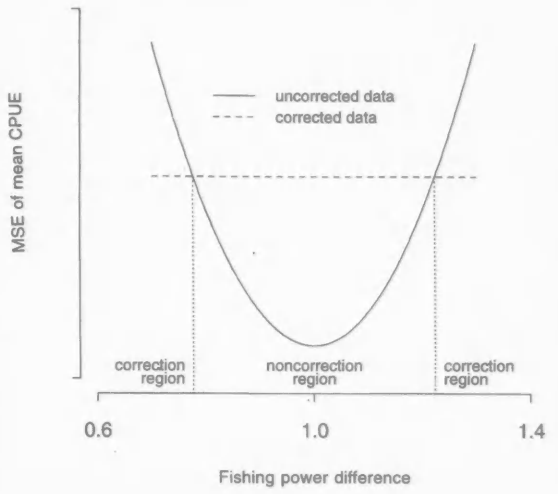

Figure 1

The noncorrection region that emerges from plotting mean square error of mean CPUE against the fishing power difference imposed on the simulated data. "Uncorrected data" refers to the scenario where mean CPUE was estimated without correcting the fishing power difference. "Corrected data" refers to the scenario where mean CPUE was estimated after correcting the fishing power difference.

Table 1

The Δ-distribution parameters and fishing power correction factors estimated from the 1992 Bering Sea survey data. Sample sizes are different because different vessels represented the "standard" vessel for each species.

	Walleye pollock (*Theragra chalcogramma*)	Flathead sole (*Hippoglossoides elassodon*)
Δ-distribution parameters		
p (fraction of zeros)	0.0336	0.1042
μ (mean of log nonzeros)	3.3590	1.5859
σ (SD of log nonzeros)	2.1194	1.4985
Number of observed CPUEs used to compute parameters	149	144
Estimated fishing power correction (FPC) factor	1.32	0.76

The Kappenman estimator of the ratio of scale parameters (Kappenman, 1992) was used to estimate the FPC in each simulated survey. Inordinately large, rare observations are typical of trawl survey CPUE data (Koeller and Smith, 1983; Weinberg et al., 1994;

Table 2

Fishing power differences imposed on the simulated data.

Catch ratio: nonstandard to standard		Catch ratio: larger to smaller
0.50	Nonstandard vessel is	2.00
0.57	half as efficient	1.75
0.67		1.50
0.71		1.40
0.77		1.30
0.80		1.25
0.83		1.20
0.87		1.15
0.91		1.10
0.95		1.05
1.00	Identical fishing power	1.00
1.05		1.05
1.10		1.10
1.15		1.15
1.20		1.20
1.25		1.25
1.30		1.30
1.40		1.40
1.50		1.50
1.75		1.75
2.00	Nonstandard vessel is	2.00
	twice as efficient	

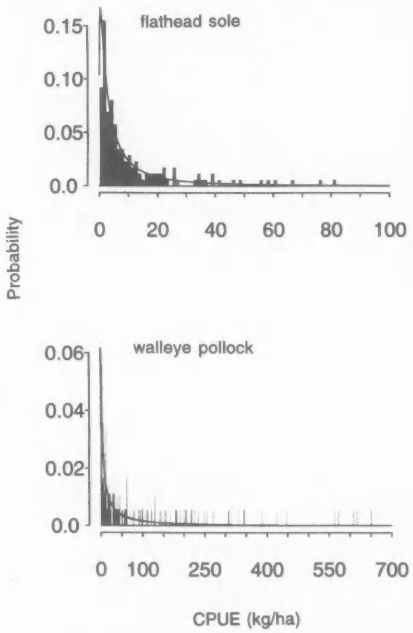

Figure 2

Histograms of catch-per-unit-of-effort (CPUE) data for flathead sole and walleye pollock overlayed by the probability density function for the Δ-distribution. The histograms are expressed as densities rather than as frequencies. The parameters specifying the Δ-distribution were estimated from the data in the histograms. The walleye pollock distribution is truncated to show reasonable detail. Not shown are the two most extreme values, 1,118.5 kg/ha and 2,906.8 kg/ha.

Goddard and Zimmermann[1]). If the rare, large observations typical of survey CPUEs are chance occurrences rather than the consequence of a fishing power difference, then a preferred estimator would be insensitive to them. The nonparametric Kappenman estimator has this property. Wilderbuer (1988) compared five FPC estimators (the ratio of means, the simple multiplicative model [Robson, 1966], the additive nested ANOVA, the multiplicative nested ANOVA, and the beta distributed index [Fanning, 1984]) and found all to have wide variability about the estimate of fishing power, indicating a sensitivity to rare large CPUEs. Wilderbuer et al. (1998) have extended this work to include the Kappenman estimator and have found it to have an estimation error equal to or lower than the others. For the Δ-distribution, s determines heaviness of the right tail of the distribution. When the Δ-distribution is more symmetric in appearance and less heavy-tailed, all of the estimators reviewed by Wilderbuer (1988) may be reasonably well-behaved. When the Δ-distribution becomes skewed to the right and the magnitude of the rare, large observations becomes quite high, the insensitivity of the Kappenman estimator results in lower estimation error.

The arithmetic mean was used as the estimator for mean CPUE because it is unbiased. Any biases observed in the means estimated in the simulations would then be due to systematic error in the data caused by fishing power differences. Also, the arithmetic mean has been argued to be the best estimator of mean CPUE (Myers and Pepin, 1990; Smith, 1990) and is commonly used (e.g., Harrison, 1992; Weinberg, et al. 1994; Goddard and Zimmermann[1]).

The issue of design-based versus model-based estimation (Smith, 1990) is raised in the choosing of the arithmetic mean to estimate mean CPUE even though the data are simulated with a probability model that has known optimal estimators. Design-based estimation is followed here because that is the strategy employed in the analysis of the Bering Sea trawl surveys. A probability model is assumed in these examples solely to provide a parameter value for estimating the MSE. In a similar vein, it would seem that the question of relative efficiency could be

answered analytically rather than through a simulation, given a known probability model. Such a solution would be difficult or impossible because of the complicating factor of the estimated FPC. Even if a model-based estimation strategy were acceptable for estimating mean CPUE from uncorrected data, the appropriate probability model for the corrected data is not clear, especially if, as in these examples, the FPC estimator has an unknown distribution.

In this example, the two sets of simulated CPUE (standard and nonstandard prior to imposing the assumed fishing power difference) are independent and identically distributed random variables. This simulation ignored the possibility for spatial correlation among observations in a real survey. Because each station in the standard Bering Sea survey is 20 n mi from its nearest neighbor, I assumed that spatial correlation was negligible and did not attempt to build it into the simulations. This is consistent with current treatment of data collected on these surveys. A more complex procedure would be needed to simulate surveys with spatial correlation among observations.

Results

For flathead sole, with a sample size of 144 per vessel, a clear region of increased error, the noncorrection region, appeared between approximately 0.77 and 1.14 in plots of MSE against the fishing power difference (Fig. 3A). The lowest MSE occurred with uncorrected data when there was identical fishing power (the value 1.0 on the x-axis). The FPC estimated for the original data, 0.76 (Table 1), fell just outside this region.

With a sample size of 50 per vessel, a clear noncorrection region appeared between approximately 0.56 and 1.19 for flathead sole (Fig. 3B). The FPC for the original data fell within this region. The minimum MSE occurred with uncorrected data. This minimum occurred, however, when the nonstandard vessel had a CPUE of about 23% less than that of the standard vessel rather than when the vessels had identical efficiencies (fishing power difference ratios of 0.87 and 1.0, respectively). The noncorrection region was also clearly asymmetric to the left with respect to a fishing power difference ratio of 1.0.

For walleye pollock, with a sample size of 149 per vessel, the noncorrection region was not as clearly defined because the lower bound occurred at some value less than 0.50; the upper bound was approximately 1.05 (Fig. 3C). The FPC estimated for the original data, 1.32 (Table 1), fell outside this region. The minimum MSE occurred with uncorrected data at a fishing power difference ratio near 0.67, where the nonstandard vessel caught 33% less than the standard. The noncorrection region was extremely

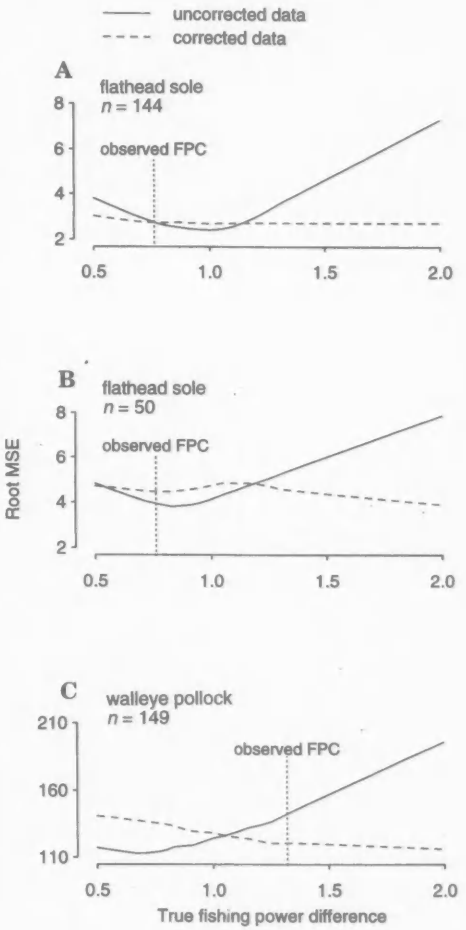

Figure 3

Simulation results: square root of the mean square error (MSE) of mean catch per unit of effort (CPUE) plotted against the true fishing power difference. The fishing power difference is expressed as the ratio of the true CPUE for the standard vessel over the true CPUE of the nonstandard vessel. "Corrected data" refers to MSEs computed from data in which the fishing power difference had been corrected. "Uncorrected data" refers to MSEs computed from data in which the fishing power difference had not been corrected. Sample size, n, refers to the number of stations realized for each vessel in each simulation. To illustrate general trends these results were smoothed with a scatterplot smoother called "lowess" in the statistical software package S-Plus (Becker et al., 1988).

asymmetric to the left with respect to a fishing power difference ratio of 1.0.

Discussion

It is a well-established ideal to choose among estimators on the basis of their relative errors. These examples demonstrate that the approach can be functional in practice as well as in the abstract when deciding whether or not to apply an FPC. It is important to distinguish between the broader notion of a decision rule based on the MSE and the specifics given here as illustrations. These examples show that regions of increased and reduced MSE can be estimated. They demonstrate common features of the regions as well as ways the regions can vary. They show that the MSE strategy is functional but also underscore problems that can arise from inappropriate choices of estimators or simulation mechanisms. In all three cases a region of increased estimation error was successfully identified and each included the value 1.0, which represents identical fishing power. However, the breadth of the noncorrection region differed depending on sample and population variance. The three noncorrection regions also differed in their symmetry about the value 1.0, which was due to an interaction between the mechanism for imposing the fishing power difference on the simulated data and the sensitivity of the arithmetic mean to rare extreme observations.

CPUE variance broadened the noncorrection region. The flathead sole simulations demonstrated the effect of the sample variance, with the smaller sample size producing the broader region (Fig. 3, plots A and B). The pollock example produced a very broad region of increased error because the population variance was quite high (Table 1; Fig. 3C). These examples confirm the truism of the MSE: the greater the variance, the less important the systematic error due to a fishing power difference. The role of variance was clearly shown in the two flathead sole simulations where the FPC observed in the original survey fell within the noncorrection region for the higher variance case, and outside the noncorrection region for the lower variance case (Fig. 3, plots A and B).

Asymmetry in the noncorrection regions was a function of the simulation mechanism. However, the problem serves to reinforce the idea that high variance tends to reduce the relative importance of bias or systematic error and reduces the benefit of correcting it. Fishing power was assumed to be a simple multiplicative effect in these simulations. The variance was altered, as well as the bias, when the fishing power difference was multiplied against Δ-distributed data, an undesirable consequence. Because the arithmetic mean is sensitive, the rare, inordinately large CPUEs exert high leverage on it. This leverage itself was altered with a multiplicative fishing power difference. For the highly skewed pollock data, the change in variance was much greater than the change in bias (Fig. 4). When the standard vessel was less efficient, the uncorrected data produced a lower MSE because the fishing power difference reduced the leverage of the rare large tows, reduc-

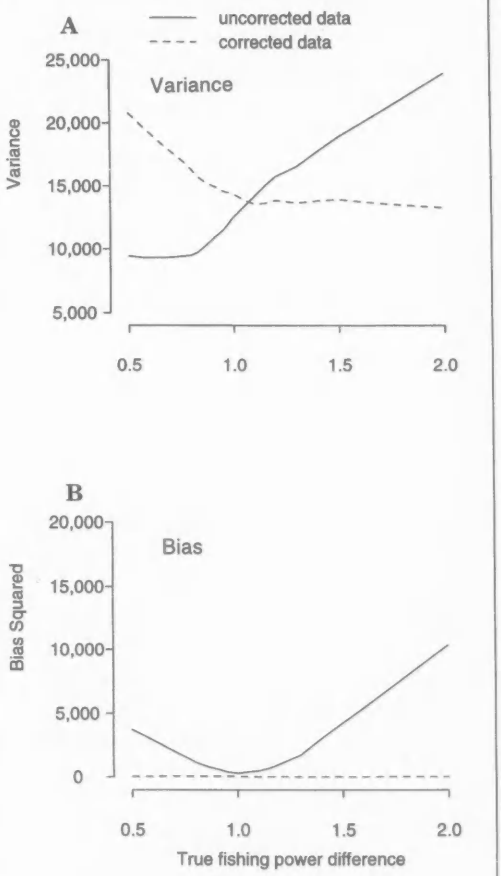

Figure 4

Components of the mean square error of the estimated mean catch per unit of effort (CPUE) of walleye pollock. "Corrected data" refers to variances and biases computed from data in which the fishing power difference had been corrected. "Uncorrected data" refers to variances and biases computed from data in which the fishing power difference had not been corrected. To illustrate general trends these results were smoothed with a scatterplot smoother called "lowess" in the statistical software package S-Plus (Becker et al., 1988).

ing the variance of the mean CPUE (Fig. 4A). The noncorrection region of data thus extended far to the left (Fig. 3C). When the nonstandard vessel was more efficient, the imposed fishing power difference had the opposite effect, increasing the variance of the mean calculated from uncorrected data (Fig. 4A). Correcting even moderate fishing power differences reduced the MSE (Fig 3C), but by reducing variance, not by correcting systematic error. This problem is purely a consequence of the fishing power mechanism in the simulations. An improved mechanism is needed to render the MSE-based decision rule a clearer tool. In this case, with highly skewed CPUE distributions, there may be a cut-off point beyond which a fishing power difference would not be imposed, because the rare, large tows are more likely to be chance occurrences than indicators of fishing power. Note that the bias did behave as expected: the uncorrected data produced a minimum when the fishing powers were identical, and corrected data produced a constant bias that was always lower than that of the uncorrected data (Fig. 4B). The pollock example illustrates how an MSE-based decision rule can be deceiving under an improperly specified model.

The noncorrection region itself is an estimate, with error around the upper and lower bounds of the range. The observed fishing power difference or correction factor will also be an estimate with its own error. Between these two sources of uncertainty, the upper and lower bounds of the noncorrection region are not as clear as they might appear in an application. Thus, a conservative approach would be to decide against using an FPC even when the observed value falls a little outside the noncorrection region. For this reason, and because improved precision generally increases certainty, it would pay to narrow the noncorrection region as much as possible through estimators with less sensitivity to the rare, large observations that characterize much CPUE data and through careful modeling of the process leading to the fishing power difference.

This decision strategy can also be used to re-evaluate old or changing fishing power problems. The concept of minimizing the MSE can accommodate changes in state-of-the-art estimation and allow the consequence of change to be examined. The decision rule remains valid regardless of improvements in simulation strategies, estimators, or understanding of processes leading to fishing power differences. The strategy can also be used to decide if experiments are warranted to calibrate the fishing power of research vessels. Such experiments tend to be very expensive yet limited in scope. Will it be possible to attain a sample size great enough to produce meaningfully narrow noncorrection regions?

A decision not to apply an FPC by these methods does not in any way imply that the fishing power difference is trivial or unimportant. For instance, if one of two vessels in a survey had a catch rate 30% lower than the other, and both vessels had equal numbers of observations, then the estimated mean CPUE could be in error by as much as 15%. An error of this magnitude could have a profound influence on a heavily exploited, closely managed stock. Yet such a fishing power difference may go uncorrected because, to correct it, would involve a risk of error of even greater magnitude. A decision against correcting is only a conclusion about the feasibility of applying an FPC, not the cost of having the systematic error in the data. Once a fishing power difference occurs in survey data, an irrevocable mistake has been made. The final estimate will have increased error, whether it is due to bias added by systematic error or due to variance added by estimating and correcting for the bias. This example illustrates the importance of maintaining standard survey techniques by illustrating the cost, in terms of precision, of correcting fishing power differences.

The decision to apply an estimated FPC is difficult. Statistical significance of a fishing power difference does not necessarily permit inference regarding the consequence of applying a correction factor when estimating mean CPUE. These three examples demonstrate the usefulness of this decision procedure. Even under difficult circumstances, high variance and an estimator sensitive to rare, large observations, the noncorrection regions are easy to defend because they are based on a clear goal—that of minimizing the error of the estimate of mean CPUE.

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Annual and between-sex variability of yellowfin sole, *Pleuronectes asper*, spring–summer distributions in the eastern Bering Sea

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Abstract.–Annual and between-sex variations in yellowfin sole, *Pleuronectes asper*, distributions in the eastern Bering Sea during spring and summer were examined by analyzing research survey data, including a standard 15-year time series from 1982 to 1996, as well as exploratory nearshore samples. Yellowfin sole were most concentrated nearshore; abundance gradually decreased with increasing bottom depth to trace numbers beyond 100 m. Male yellowfin sole were distributed nearer to shore than females in all years.. Proportions of males (no. males/no. both sexes), therefore, increased nearshore with decreasing bottom depth. Males outnumbered females by two to one in waters less than 30 m deep. Yellowfin sole during 1982–84 were distributed in deeper waters than during 1985–96. The shallower distributions after 1984 were attributed to greater percentages of mature fish that reside in nearshore spawning areas (< 30 m) during spring–summer. High biomass estimates (>3 million metric tons) during 1982–84 were attributed in part to increased availability of yellowfin sole within the standard survey area.

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Yellowfin sole, *Pleuronectes asper*, of North America has a Pacific coast distribution from British Columbia (49°N) north to the Chukchi Sea (70°N) and a distribution along the Asian coast that ranges from the Sea of Japan (35°N) north to the Gulf of Anadyr (Fadeev, 1970; Hart, 1973; Bakkala, 1981; Wilderbuer et al., 1992). The eastern Bering Sea shelf has supported the largest concentration of yellowfin sole (Bakkala, 1993), with survey biomass estimates exceeding 2 million metric tons (t) since the early 1980s (Wilderbuer et al., 1992).

Spring–summer (June–August) distributions of yellowfin sole in the eastern Bering Sea are dependent upon the timing of their annual cross-shelf migration from overwintering grounds near the shelf-slope break (about 200 m bottom depth) to nearshore waters (<50 m bottom depth) of Bristol Bay north to Nunivak Island (Bakkala, 1981; Wakabayashi, 1989). This migration is thought to follow the ice edge as it recedes during spring (Bakkala, 1981). Many juvenile yellowfin sole are likely nonmigratory and remain nearshore under ice-cover during winter (Fadeev, 1970). Juvenile and adult distributions, therefore, overlap during spring–summer when adults enter nearshore waters to spawn (Nichol, 1995, 1997).

Past yellowfin sole abundance in the eastern Bering Sea has varied with the magnitude of fishery exploitation. A predominantly foreign-led commercial trawl effort (Japan and U.S.S.R.) accounted for annual landings in excess of 400,000 t from 1959 to 1962. This trawl effort led to a decline of the stock and to significantly lower annual catches (<100,000 t) through the 1970s (Wilderbuer et al., 1992). Lower exploitation rates during the late 1970s coincided with a major increase in stock abundance that appeared to peak in the early 1980s. Considering the high abundance, annual yellowfin sole catches have been moderate since 1982, averaging 147,433 t (Table 1). Commercial trawl catches of yellowfin in recent years have been limited by fishery management time and area closures owing to bycatch of species such as Pacific halibut (*Hippoglossus stenolepis*), Pacific herring (*Clupea pallasi*), Tanner crab (*Chionoecetes bairdi*), and red king crab (*Paralithodes camtschaticus*) (Witherell, 1995). Despite moderate exploitation, annual survey biomass estimates have fluctuated widely since the early 1980s (Wilderbuer[1]). These fluctua-

[1] Wilderbuer, T. K. 1996. Yellowfin sole. Chapter 3 *in* Plan team for groundfish fisheries of the Bering Sea/Aleutian Islands (ed.), Stock assessment and fishery evaluation

continued on next page

Table 1

Standard AFSC survey yellowfin sole (*Pleuronectes asper*) biomass and population estimates, percentage of male and female CPUE (kg/hectare) in nearshore (<30 m bottom depth) waters, sex-proportions, and mean CPUE-weighted bottom depths by sex, for years 1982–96. Commercial catch estimates for yellowfin sole in the eastern Bering Sea are also included.

Year	Survey biomass (metric tons)	% CPUE[1] < 30 m		Population numbers (billions)	Proportion male (m/m+f)[2]	Mean depth (m)[3]		Commercial catch (metric tons)[4]
		Males	Females			Males	Females	
1982	3,377,838	20.56	9.81	20.67	0.492	45.0	52.9	95,712
1983	3,535,269	22.04	5.41	16.94	0.486	46.3	58.5	108,385
1984	3,141,188	16.96	5.62	14.26	0.434	47.3	58.7	159,526
1985	2,443,666	29.63	11.39	10.60	0.437	43.3	55.2	227,107
1986	1,909,866	31.05	13.38	7.96	0.436	42.8	54.7	208,597
1987	2,613,067	27.47	13.18	10.35	0.438	44.6	53.6	181,428
1988	2,402,369	23.94	9.86	10.09	0.426	45.0	55.6	223,156
1989	2,316,249	28.83	20.05	9.66	0.454	42.3	48.3	153,165
1990	2,183,708	24.30	12.46	9.06	0.435	44.6	53.0	83,970
1991	2,393,268	19.22	5.94	9.54	0.453	44.5	53.8	115,842
1992	2,172,900	34.89	19.01	8.21	0.452	42.3	53.4	149,569
1993	2,465,443	31.64	11.59	10.03	0.442	43.8	54.2	106,101
1994	2,610,474	32.34	13.73	10.70	0.442	40.1	51.0	144,544
1995	2,009,671	33.02	13.66	8.24	0.445	40.2	51.3	124,740
1996	2,298,560	31.28	9.83	9.62	0.460	43.9	56.8	129,659

[1] $\%CPUE=(\sum CPUE_{i,d<30}/\sum CPUE_{i,d=all}) \times 100$ where $CPUE_{id}$ = station CPUE of the ith sex within the dth depth range. Note that this estimate is derived from the AFSC survey which did not cover the entire nearshore area.
[2] Proportion male = population number of males divided by population number of males and females.
[3] Mean depths are weighted by CPUE (kg/hectare) values at each tow location.
[4] Total retained and discarded catch estimates for yellowfin sole from foreign (1982–87), joint-venture (1982–90), and domestic (1987–present) fisheries in the eastern Bering Sea (Wilderbuer[1]).

tions are inconsistent with age-structured stock synthesis models (Methot, 1990) that predict relatively stable abundance levels after 1981 (Wilderbuer[1]).

Large scale spring–summer Alaska Fisheries Science Center (AFSC) resource assessment surveys of the eastern Bering Sea shelf began with a baseline survey in 1975 (Pereyra et al.[2]) and have continued annually since 1979 with the primary purpose of estimating the abundance of important groundfish and crab species, including yellowfin sole (Gunderson, 1993). In 1982, a change in the standard survey trawl from a 400-mesh "eastern" trawl to a larger 83–112 "eastern," increased the catch efficiency for most flatfish species including yellowfin sole (Bakkala, 1993). Survey gear has remained constant since 1982. Although these surveys cover most of the shelf area north of the Alaska Peninsula and south of latitude 60°N (Fig. 1), nearshore waters have been excluded owing to shallow bottom depths and variable bottom substrate. Areas such as Togiak Bay (Fig. 1), where commercial trawlers have successfully targeted yellowfin sole in waters as shallow as 5–6 m (Low and Narita, 1990), have been excluded from resource assessment. Recognition that yellowfin sole spawn during the survey period (June–August) and that nearshore spawning grounds extend into these nonsurveyed areas (Nichol, 1995) has prompted speculation as to whether fluctuations in survey biomass may be due to annual variation in yellowfin sole distributions that overlap surveyed and nonsurveyed areas.

This study investigates two potential sources of variation in yellowfin sole distribution during spring-summer, which may partially account for fluctuations in survey biomass estimates. In this paper, I describe variations in yellowfin sole distribution patterns between sexes and among years. Data from exploratory nearshore samples are included to demonstrate problems associated with the exclusion of nearshore areas from resource assessments.

[1] (*continued from previous page*) report for the groundfish resources of the Bering Sea/Aleutian Islands region as projected for 1997. North Pacific Fishery Management Council, 605 W. 4th Avenue Suite 306, Anchorage, AK 99501.

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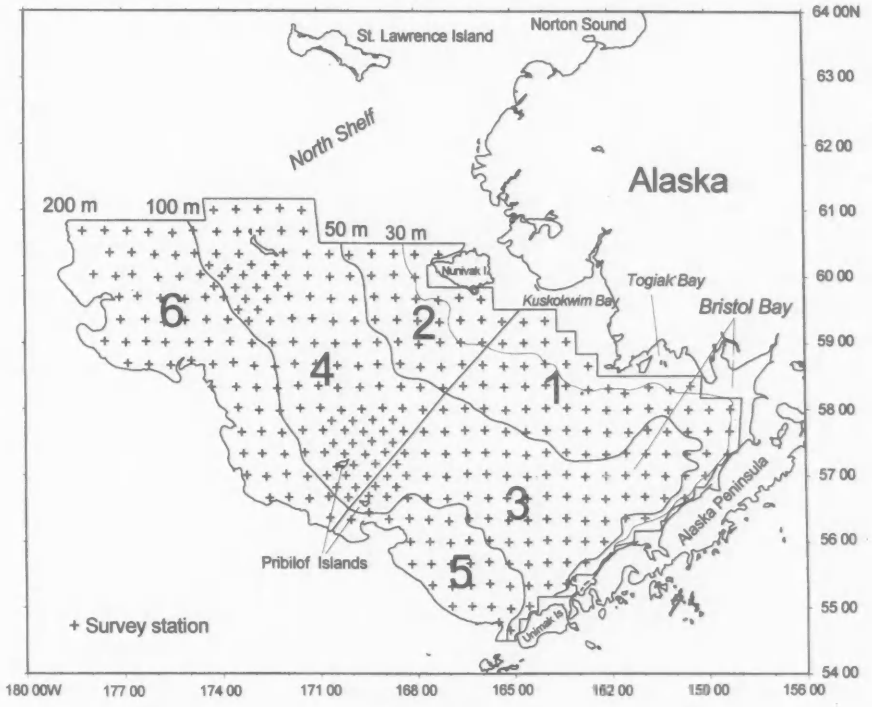


Figure 1

Standard Alaska Fisheries Science Center eastern Bering Sea survey stations. Large numerals (1–6) indicate strata areas: strata 1–2, <50 m; strata 3–4, 50–100 m; strata 5–6, 100–200 m.

Materials and methods

Surveys and gear

Standard AFSC Owing to differences in standard trawl gear used prior to 1982, only the 1982–96 standard surveys are considered here. About 350 standard stations, ranging in depth from 16 m to 230 m, were sampled annually for each of the 1982–96 AFSC surveys (Fig. 1; Table 2). Survey stations were spaced 37 km (20 nautical miles) apart, following a 37 × 37 km grid pattern. Surveys generally began in inner Bristol Bay, followed transects directed north and south, and progressed east to west with each finished transect. Trawls were towed for about 30 min at a speed of 5.6 km/h (3 knots) at each station during daylight hours. The standard AFSC sampling gear, an 83–112 "eastern" trawl, was characterized by average vertical and horizontal wing openings of 2.6 m and 16.5 m, respectively. Effective net spread and height measurements were obtained by means of a commercial trawl net-mensuration system (Scanmar) that was used during most tows. Footrope and headrope lengths were 25.3 m and 34.1 m, respectively. Paired 55-m dandylines (bridles) were attached to each wing and to 1.8 m × 2.7 m steel V-doors. Chain extensions measuring 61 cm in length were attached from each end of the footrope to the lower dandyline to improve bottom contact of the footrope. Two chartered commercial trawl vessels were employed each year to complete the standard survey. A total of 9 vessels ranging from 30.0 to 39.6 m in length have been used since 1982.

Total yellowfin sole catch weights (kg) as well as random sex-specific length-frequency samples (total length in cm) were collected at each station (haul) where the species was captured. Haul positions, bottom depths, and surface and bottom temperatures were also recorded at each station.

AFSC exploratory tows Additional 30-minute tows in waters nearer shore than the standard survey area were made during the course of the AFSC surveys with the same trawl gear and sampling procedures. Sampling depths ranged from 9.0 m nearshore to 29.3 m offshore. A total of twenty-five nearshore tows, 13 in the Togiak Bay area and 12 in the Kuskokwim Bay area, were made during the 1988–91 standard

Table 2

Summary of AFSC groundfish surveys on the eastern Bering Sea shelf. Tows in which yellowfin sole (YFS, *Pleuronectes asper*) were captured are noted parenthetically.

Survey	Area[1]	Gear[2]	Date	Bottom depth (m)	Number of tows[3]	Number of YFS measured
Standard	EBS	83-112	June–Aug 1982	18–137	329 (251)	37,023
			June–Aug 1983	20–134	354 (270)	33,924
			June–Aug 1984	18–134	355 (279)	33,894
			June–Aug 1985	18–154	353 (270)	33,824
			June–Aug 1986	18–148	354 (251)	30,470
			June–Aug 1987	18–112	342 (235)	31,241
			June–Aug 1988	18–130	353 (249)	27,121
			June–Aug 1989	18–110	354 (236)	29,510
			June–Aug 1990	16–126	352 (247)	30,491
			June–Aug 1991	18–119	351 (248)	27,985
			June–Aug 1992	16–152	336 (231)	23,626
			June–Aug 1993	18–163	355 (243)	26,647
			June–Aug 1994	16–113	355 (257)	24,420
			June–Aug 1995	16–154	356 (249)	22,111
			June–Aug 1996	20–114	355 (247)	27,190
Exploratory	Kuskokwim Bay area	83–112	June 1988	13–27	4 (4)	786
			June 1989	9–20	4 (4)	734
			June 1990	13–29	2 (2)	408
			June 1991	13–29	2 (2)	293
	Togiak Bay area	83-112	June 1988	13–29	5 (5)	1264
			June 1989	16–27	5 (5)	1438
			June 1990	11–26	2 (2)	515
			June 1991	15	1 (1)	107
Nearshore beam trawl	Togiak Bay area	PSB	May, 1995	2–30	28 (28)	4134

[1] EBS = eastern Bering Sea shelf area from the Alaska Peninsula north to latitude 62° N.
[2] 83-112 = Eastern otter trawl with 25.3 m (83 ft) headrope and 34.2 m (112 ft) footrope. PSB = plumb-staff beam trawl with a 3.1 m (10 ft) aluminum beam.
[3] Number in parentheses indicates number of tows in which yellowfin sole were captured.

surveys (Fig. 2; Table 2). These tows were conducted to collect preliminary data on spawning yellowfin sole, which were known from commercial trawl reports to occur in these nearshore areas. Extensive survey coverage of this area has been limited owing to the shallow bottom depths.

Nearshore beam-trawl survey A 3.1-m plumb staff beam trawl with specifications detailed in Gunderson and Ellis (1986) was used aboard a chartered 9.7-m (32-ft) purse-seine or gillnet vessel. This survey successfully sampled a total of 28 stations in the shallow waters of the Togiak Bay area, from 18 May to 28 May 1995 (Fig. 2; Table 2). Sampling depths ranged from 1.8 m nearshore to 30.2 m offshore. Tows were made during daylight hours and were less than 10 min in duration. All yellowfin sole were sexed, measured, and assigned a maturity code. For the purpose of this examination, maturity was classified as either mature or immature. Females were considered mature if ovaries were yolked or recently spent. Males were considered mature if testes were swollen, opaque colored, running with sperm, or recently spent.

Analysis

Yellowfin sole distributions were described in terms of catch per unit of effort (CPUE; kg/hectare) for each of the 1982–96 AFSC standard surveys. Calculation of CPUE followed area-swept methods described by Alverson and Pereyra (1969), whereby catch is the total weight (kg) of yellowfin sole within a station tow and effort is the area (hectare) swept by the path of the trawl. Area swept was computed as the product of the distance fished and the effective net-spread

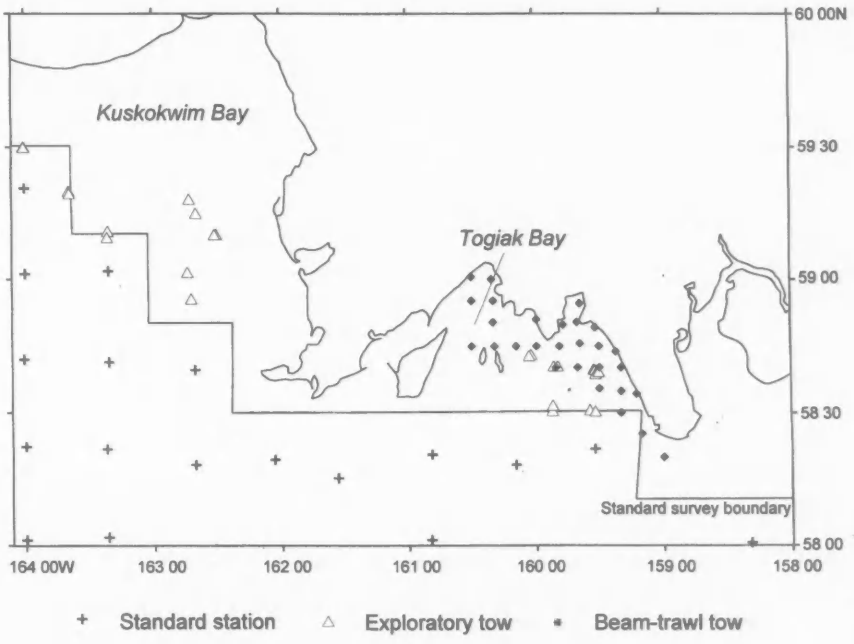


Figure 2

Geographic location of exploratory (1988–91) and beam-trawl tows (1995) made inshore of the standard AFSC survey stations.

for each tow. All fish within the path of the trawl were assumed captured. Male and female catch rates at each station were calculated as follows:

$$CPUE_i = CPUE \cdot (Weight\ Proportion\ of\ ith\ sex) = CPUE \cdot \left(\frac{\sum_{j=1}^{n_i} aL_{ij}^b}{\sum_{j=1}^{n} aL_j^b} \right), \quad (1)$$

where $CPUE$ = catch per unit of effort (kg/hectare) of all yellowfin sole at a station;
$CPUE_i$ = catch per unit of effort (kg/hectare) of the ith sex;
n = total number of fish;
n_i = number of fish of the ith sex;
L = total length (cm) of the jth fish, males and females included;
L_i = total length (cm) of the jth fish and ith sex;
a = 0.007441; and
b = 3.130.

Constants a and b were calculated with nonlinear regression (nlin procedure; SAS Institute, 1989) with the equation: $W = aL^b$ (n=796, r^2=0.99), where W=individual yellowfin sole weights (g) measured during the 1987 standard AFSC survey. Prior to estimating a and b, a test comparing the length-weight relations between males and females was performed. A test of the null hypothesis of no difference between male and female linear log(length)-log(weight) revealed no significant difference in either slopes (analysis of covariance; F=2.46; df=1,792; P=0.12) or intercepts (F=2.05; df=1,793; P=0.15). Sexes were therefore combined to estimate constants a and b above.

Annual yellowfin sole "survey biomass" was estimated as:

$$Biomass = \sum_{k=1}^{n} \left(\overline{CPUE}_k \cdot A_k \right), \quad (2)$$

where $\overline{CPUE}_k$ = the mean of station CPUE values (Eq. 1) within the kth stratum (Fig. 1); and
A_k = the area (hectares) of the kth stratum.

Proportions of males (no. males/no. both sexes) at each station were averaged across stations by depth

group (10–19 m, 20–29 m, etc.), weighted by the station CPUE (no. fish/hectare). For nearshore beam-trawl samples, variance surrounding mean male-proportions was estimated following Cochran (1977) for estimation of proportions in cluster sampling. For standard and exploratory surveys, the error structure of proportion means was approximated by the boot-strap method (Efron and Tibshirani, 1993). The station-specific data were randomly resampled and the mean estimated 1000 times. Twenty-fifth and 975th quantiles were chosen for the 95% confidence bounds.

Results

Between-sex variation

Male yellowfin sole within the standard survey area were distributed closer to shore than were females in all years, 1982–96 (Fig. 3; Table 1). In addition to having an overall distribution in deeper water, females also appeared to have a more extended northwesterly distribution than males (Fig. 3). Males outnumbered females near shore, whereas farther off shore (>60 m bottom depth), females outnumbered males (Fig. 4). The proportion of males (no. males/no. both sexes) and CPUE increased with decreasing depth (Fig. 4). Togiak and Kuskokwim Bay area samples from exploratory trawls were also characterized by a higher proportion of males as well as greater overall yellowfin sole concentrations. The proportion of males from Togiak and Kuskowim Bay areas averaged 0.60 and 0.67, respectively (Fig. 4).

Sex proportions also varied between mature and immature yellowfin sole. Among beam-trawl samples from the Togiak Bay area (Fig. 2), the overall mean proportion of males was 0.54 (SE=0.0033). Among mature fish, however, the proportion of males averaged 0.65 (SE=0.0067) and among immature fish, mostly small <20 cm fish, the proportion of males averaged 0.50 (SE=0.0024). Within the spawning area (<30 m), the proportion of males among mature fish averaged 0.68 (SE=0.0056) (Fig. 5).

Among-year variation

Yellowfin sole spring–summer distributions varied from year to year, although the most notable difference was for years 1982–84 when distributions of males in particular within the standard AFSC survey area were shifted off shore (deeper waters) relative to subsequent years (1985–96) (Fig. 3). A greater mean CPUE-weighted bottom depth in conjunction with a decreased percentage of nearshore (<30 m) CPUE (kg/hectare) during 1982–84 confirmed a bathymetric shift to deeper waters for both male and female distributions in relation to subsequent years (Table 1). Interestingly, yellowfin sole biomass levels, as well as the overall proportion of males within the standard AFSC survey, were considerably higher during 1982–83 than in subsequent years (Table 1).

Discussion

Between-sex variation

Distributional differences between male and female yellowfin sole exist primarily because males mature earlier than females. Standard AFSC surveys, exploratory nearshore samples, and Togiak area beam-trawl samples have shown conclusively that male yellowfin sole outnumber females in the nearshore areas (<30 m bottom depth) of the eastern Bering Sea during spring–summer. Given that males mature approximately 4 years earlier than females (Wilderbuer et al., 1992), spawning males should considerably outnumber spawning females. Because yellowfin sole spawn primarily in nearshore areas (<30 m) during spring–summer (Nichol, 1995), mature males outnumber mature females by nearly 2:1 in this region. In deeper waters, females outnumber males because of the abundance of larger (25–32 cm TL) immature females that generally do not move into the spawning area (Nichol, 1997).

Factors such as differential life-spans and differential catchability between sexes have been shown to cause similar sex-ratio patterns in other species (Beverton, 1964). Such factors were assumed negligible in this case. Since 1982, maximum ages for yellowfin sole males and females averaged 25.7 and 26.1 years,[3] respectively, and have not differed significantly (paired t-test; P-value=0.7758, df=28), suggesting similar life-spans for males and females. Beverton (1964) discussed the potential effects of differential natural mortality, fishing mortality, and catchability on sex-ratios of plaice (*Pleuronectes platessa* L.) in the North Sea. The possibility that male yellowfin sole may be more readily captured by trawl gear, at least among immature fish, is unlikely given that the sex proportion among immature fish in the spawning area was near 0.5 (Fig. 5). The possibility that spawning males are more catchable than females owing to differential spawning behavior, as Beverton (1964) reported for plaice, is not known for

[3] Ages were determined by the Age and Growth Unit of the Alaska Fisheries Science Center (AFSC) from annual otolith collections made during the standard AFSC groundfish trawl surveys in the eastern Bering Sea.

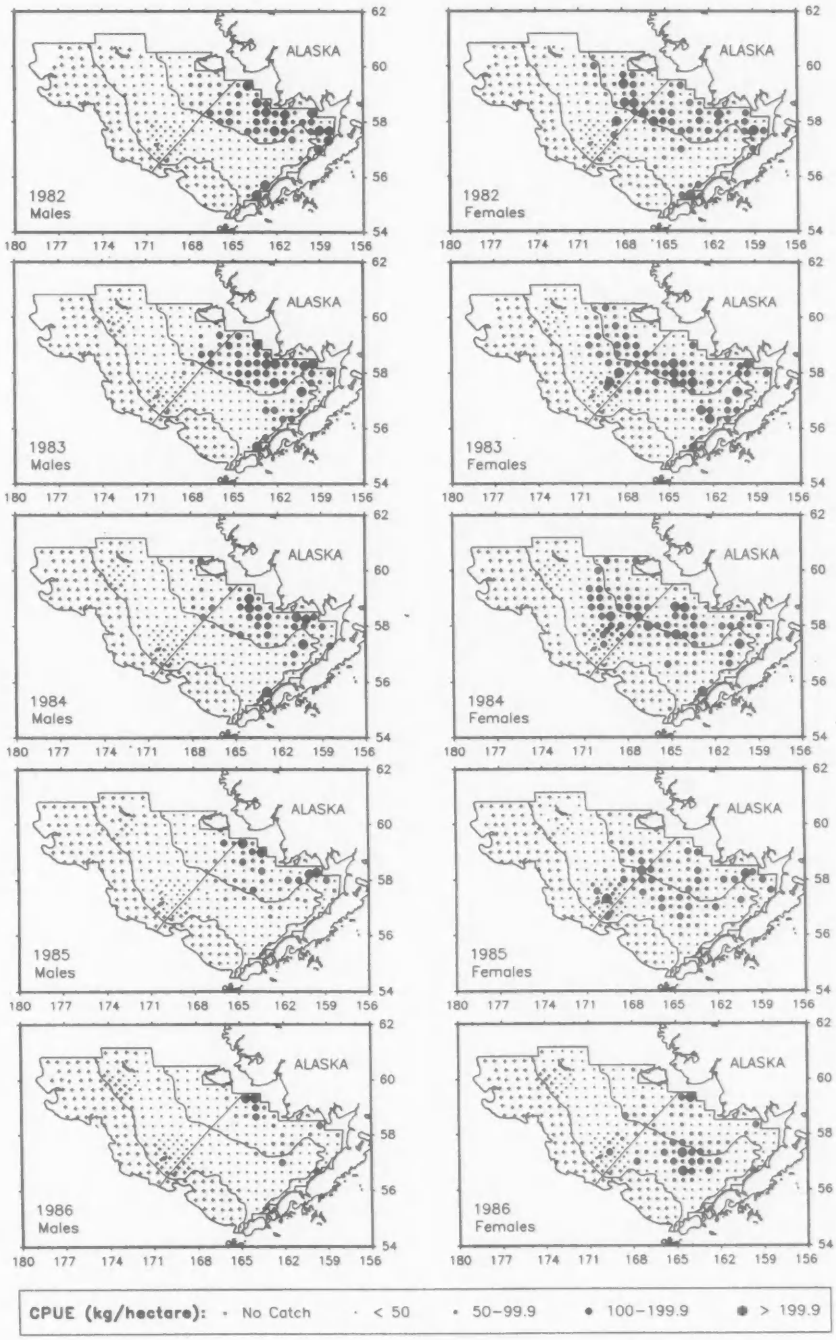
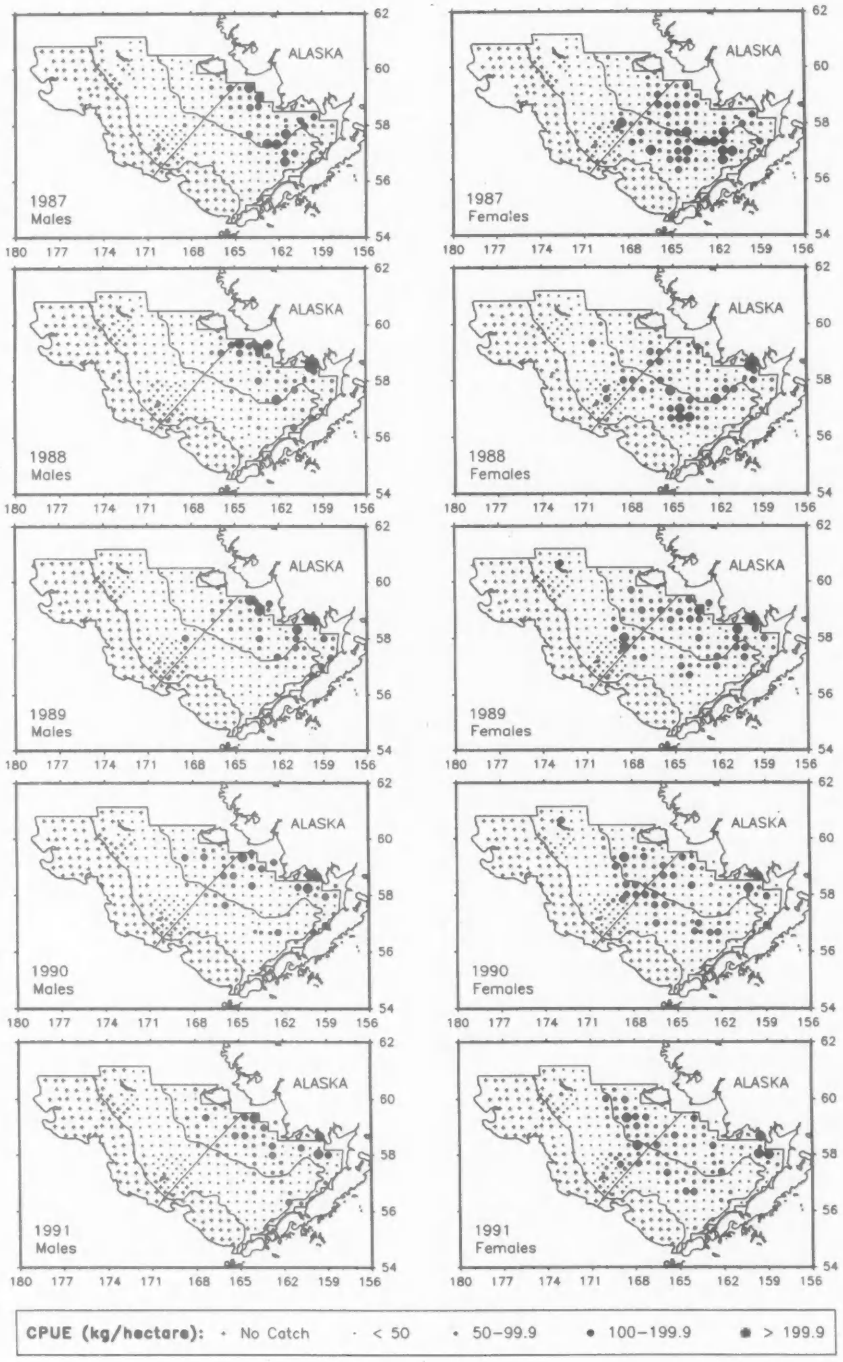


Figure 3

Geographical distribution of male and female yellowfin sole (*Pleuronectes asper*) in terms of catch per unit of effort (CPUE; kg/hectare) for each year, 1982–96.



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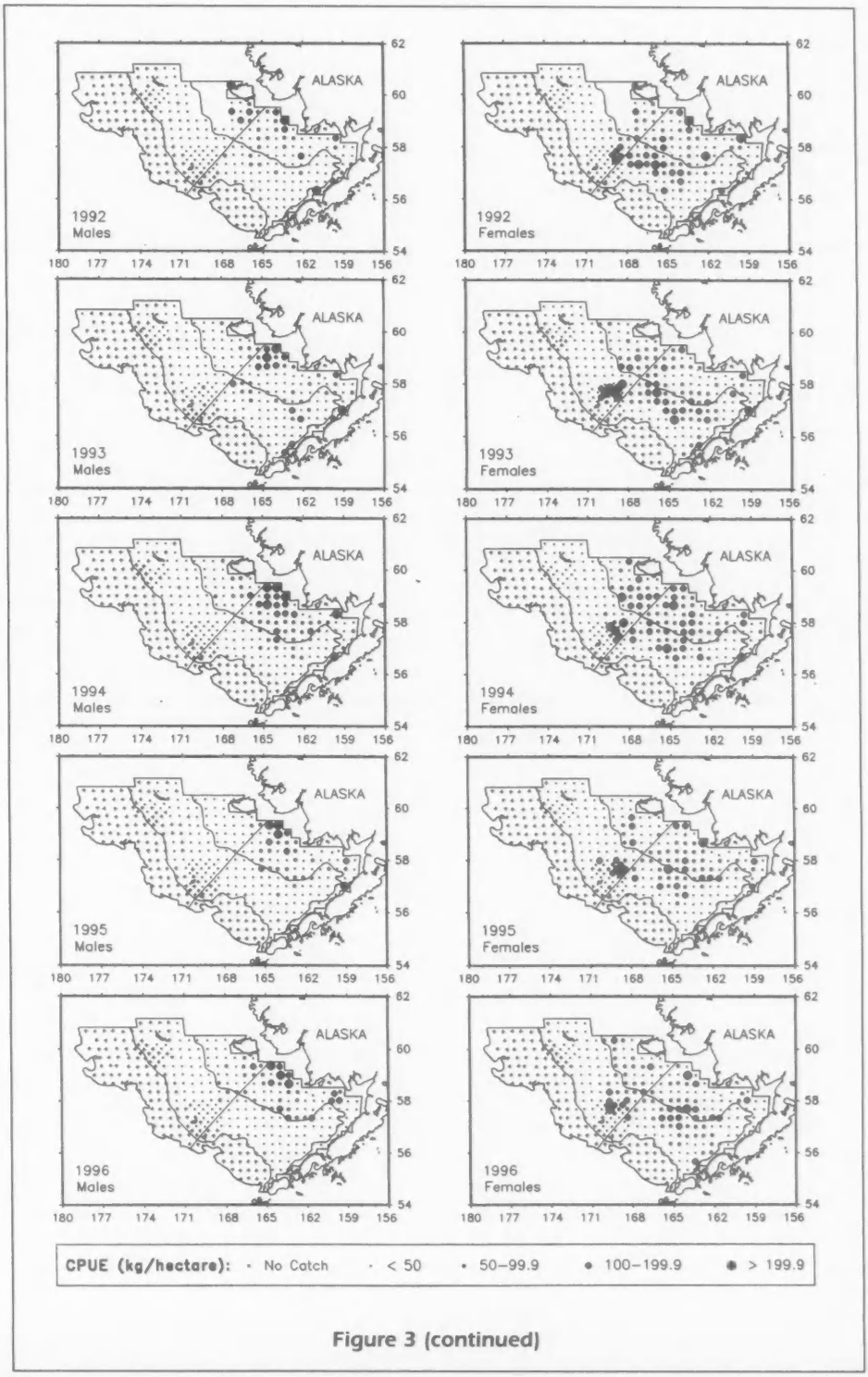

Figure 3 (continued)

yellowfin sole. However, because yellowfin sole males were dominant inshore and females were dominant offshore, the more likely cause for the sex-proportion patterns observed here was the differential distribution patterns between sexes.

Among-year variation

Spring–summer distributions during 1982–84 may have been deeper than those in subsequent years, in part, because the population was younger and less mature. Wilderbuer et al. (1992) indicated that older (>17 years) yellowfin sole were an insignificant part of the population prior to the mid-1980s compared with later years and indeed, length distributions were skewed toward smaller length groups during the 1982–84 surveys compared with later years (Fig. 6). Given estimated lengths at 50% maturity of 20.3 and 28.8 cm TL for male and female yellowfin sole, respectively (Wilderbuer et al., 1992), many of the fish constituting the strong modes from 1982 to 1984 were sexually immature. Certainly there was a progression from immaturity to maturity for many of these fish. Nichol (1997) showed that larger (25–32 cm) immature females nearing maturity maintain a deeper bathymetric distribution than mature spawning fish during spring–summer. With increasing maturity of the population, therefore, we would expect to see a distribution shift to shallower spawning waters in years after 1984. Smaller males (22–27 cm TL) and females (25–32 cm TL) constituted a large proportion of the yellowfin sole biomass from 1982 to 1984 (Fig. 7). High concentrations of 22–27 cm males that resided at 40–49 m bottom depth during 1982–84 were not apparent from 1985 to 1996. Similarly, prominent modes of 25–32 cm females at 30–39 m and 70–79 m depths during 1982–84 were not nearly as apparent during 1985–96 (Fig. 7).

Why then was the proportion of males within the standard area higher during 1982–83 than other years? The most plausible explanation is that the deeper overall yellowfin sole distributions during these years rendered the population more available to the survey. Nearshore areas not

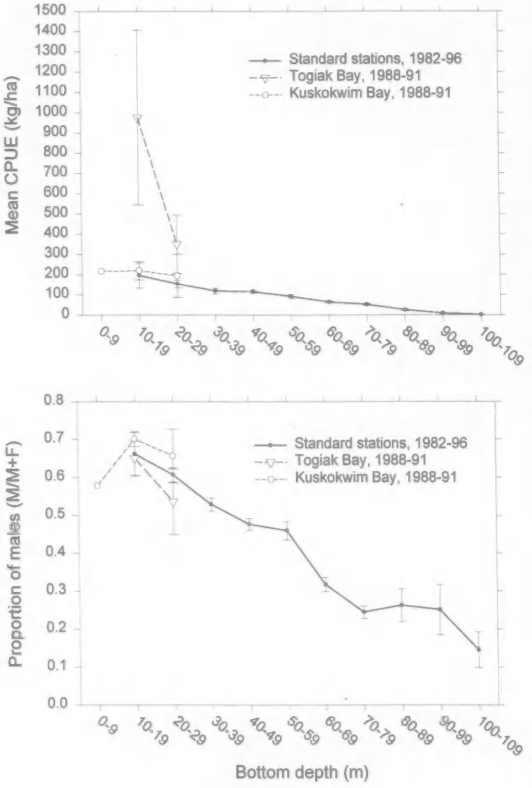

Figure 4

Mean catch per unit of effort (CPUE; kg/hectare) and mean proportion of males (no. males/no. both sexes) of yellowfin sole (*Pleuronectes asper*) at standard Alaska Fisheries Science Center trawl stations (1982–96) and at sites in nearshore Togiak Bay and Kuskokwim Bay areas (1988–91). Mean proportions are weighted by the CPUE (no. fish/hectare) at each station within each depth grouping. Bars are 95% confidence intervals.

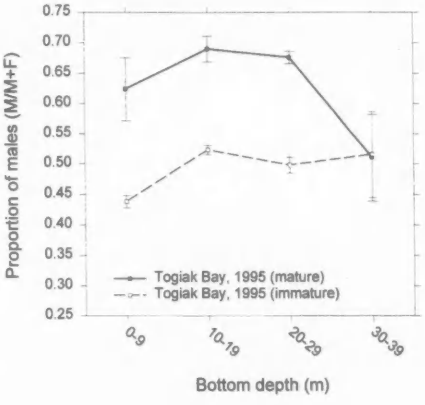

Figure 5

Mean male proportions (no. males/no. males and females) of mature and immature yellowfin sole (*Pleuronectes asper*) by bottom depth during the 1995 beam-trawl survey of Togiak Bay. Mean proportions are weighted by the CPUE (no. fish/hectare) at each station within each depth grouping. Bars are 95% confidence intervals.

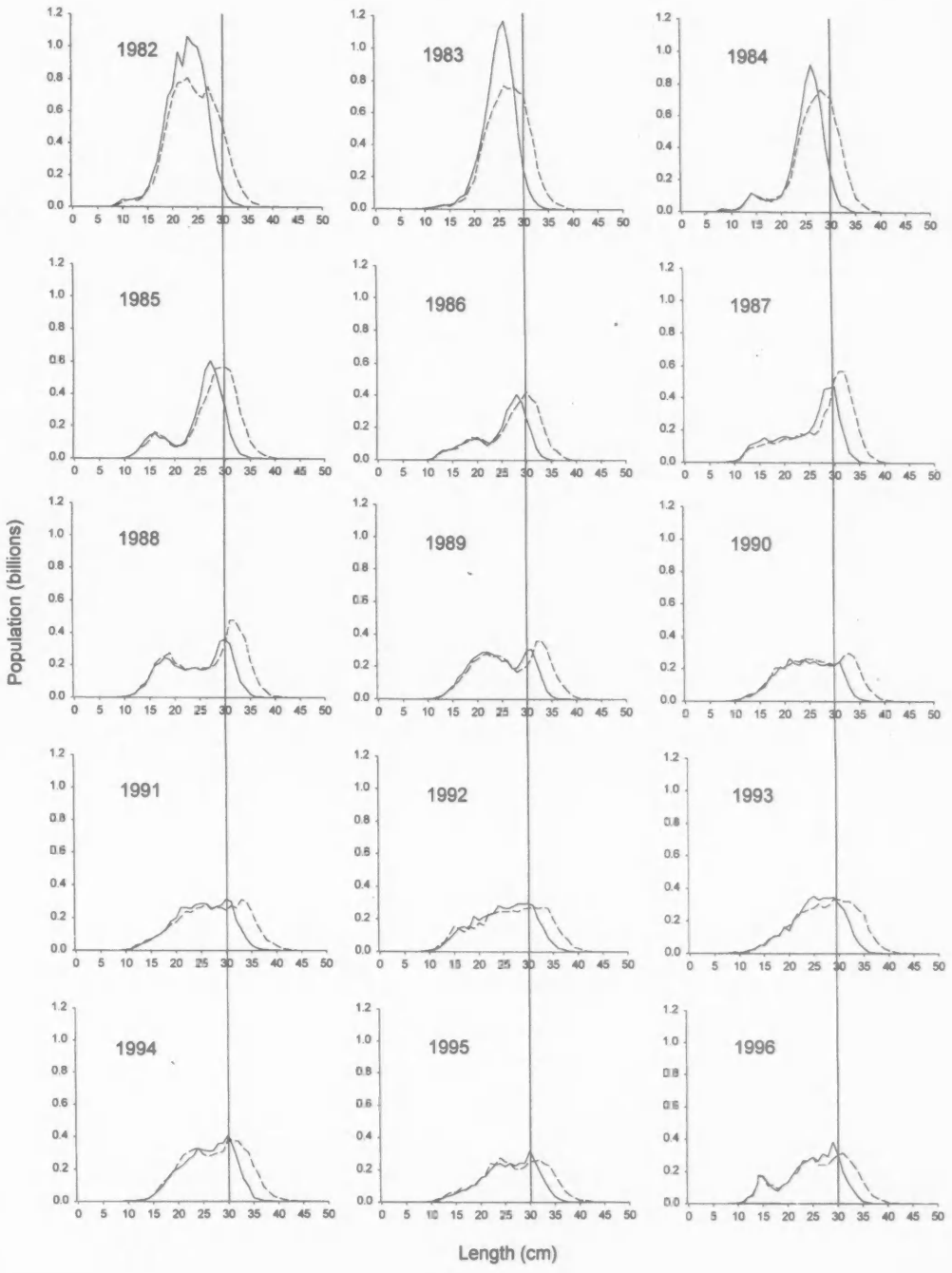

Figure 6

Length composition of male (solid line) and female (dashed line) yellowfin sole (*Pleuronectes asper*) in terms of population numbers for years 1982–96. The vertical lines provide a reference for fish length at 30 cm TL.

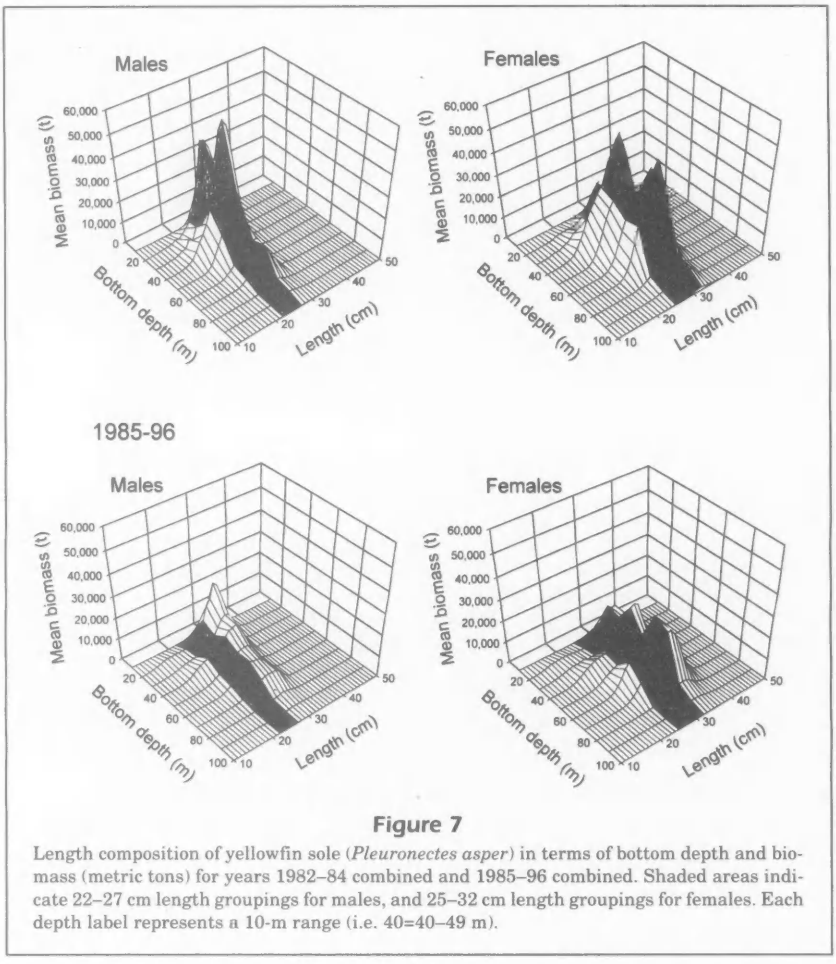

Figure 7

Length composition of yellowfin sole (*Pleuronectes asper*) in terms of bottom depth and biomass (metric tons) for years 1982–84 combined and 1985–96 combined. Shaded areas indicate 22–27 cm length groupings for males, and 25–32 cm length groupings for females. Each depth label represents a 10-m range (i.e. 40=40–49 m).

sampled during the standard AFSC surveys likely contained more males than females. Hence, a shift of the population to deeper waters possibly exposed a higher proportion of males to the survey gear than during subsequent years.

Effects of distribution on survey biomass

Given that the standard AFSC survey area does not encompass the entire yellowfin sole distribution, annual distributional shifts between surveyed and nonsurveyed areas may explain the annual biomass fluctuations observed within the standard AFSC survey area. Yellowfin sole biomass estimates within the standard AFSC survey area have fluctuated from a high of 3.5 million t in 1983 down to 1.9 million t in 1986 (Table 1). These fluctuations are not possible according to yellowfin sole life history and the relatively light fishing exploitation of this species since the late 1970s (Wilderbuer et al., 1992). Stock synthesis models based on catch-at-age data (Methot, 1990) predict much more stable changes in yellowfin sole biomass (Fig. 8). Even though these models incorporate survey biomass estimates as auxiliary information (Wilderbuer[1]), predicted biomass estimates from 1982 to 1984 were much lower than what survey estimates indicated. I propose that the deeper overall spring–summer distributions from 1982 to 1984 contributed to an inflation of survey biomass estimates in contrast with subsequent years, owing to increased availability of yellowfin sole to the AFSC survey. Strong year classes that were present in the survey area during 1982–84 may have become less accessible to the survey gear during later years owing to their sexual maturation and subsequent migration into shallower nearshore spawning waters.

Nearshore areas from the standard survey boundary to the coastline (excluding river systems and in-

ner bays) totaled approximately 40,184 km^2 (Fig. 1). In contrast, the two nearest shore strata within the AFSC survey area total 77,871 km^2 (stratum 1) and 41,027 km^2 (stratum 2), respectively. The coastline areas, thus, offered yellowfin sole a considerable refuge from the AFSC bottom trawl survey. According to past samples from Togiak Bay and Kuskokwim Bay areas (Table 2), yellowfin sole are more concentrated in the coastline areas than within the standard AFSC survey area (Fig. 4). Considering the vast unsampled areas near shore, as well as the large yellowfin sole concentrations that inhabit these areas, annual fluctuations in biomass within the standard AFSC area should be expected.

Biomass estimates generated from standard AFSC eastern Bering Sea trawl surveys are considered a relative measure of population abundance. However, because nonsurveyed nearshore areas contain higher concentrations of yellowfin sole and because males outnumber females there, standard area biomass estimates underestimate male abundance. Distribution plots suggest a more extended northwesterly distribution of females compared with males. Within the northwest area (subareas 2, 4, and 6) the average proportion of males from 1982 to 1996 was 0.33 ± 0.016 (95% confidence) compared with 0.50 ± 0.010 in the southeast area (subareas 1, 3, and 5). The lack of males in the northwest area may be an indication that a large percentage of males missed by the survey inhabit nearshore waters of Kuskokwim Bay and waters east of Nunivak Island (Fig. 1).

Bottom temperature may be one factor that has influenced the availability of yellowfin sole to the standard AFSC survey. Except for the years 1982–84, when fish availability was affected more by population structure, biomass estimates were generally lower during colder years (Fig. 9). Midshelf bottom temperatures were chosen to represent annual temperature regimes because water exchange is minimal when compared with the inner shelf (< 50 m) and outer shelf (>100 m) waters (Coachman, 1986; Wilderbuer et al., 1992). Distribution patterns, as well as timing of the annual yellowfin sole cross-shelf migration, may in part be dependent upon the annual temperature regime. Fadeev (1965) indicated that spring yellowfin sole migrations occurred one month earlier than usual during years when warm water developed earlier on the eastern Bering Sea shelf. Pola et al. (1985) also demonstrated, using simulation models, that summer yellowfin and rock sole distributions could be established two months earlier in a warm year than in a cold year. If ice-edge

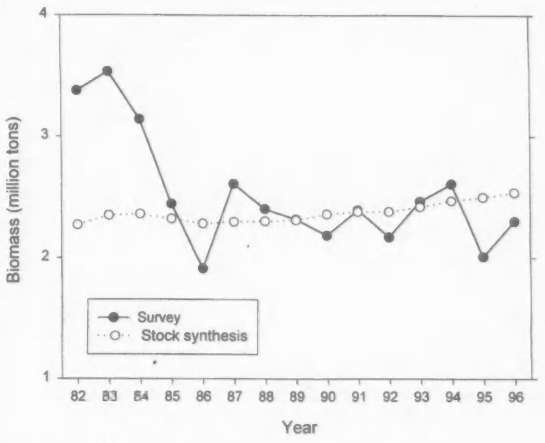

Figure 8

Comparison of yellowfin sole (*Pleuronectes asper*) biomass estimates from the AFSC survey and from stock synthesis analysis. Stock synthesis estimates incorporate the selectivity of the survey sampling gear and use survey biomass estimates as auxiliary data, but they are based on catch-at-age-data.

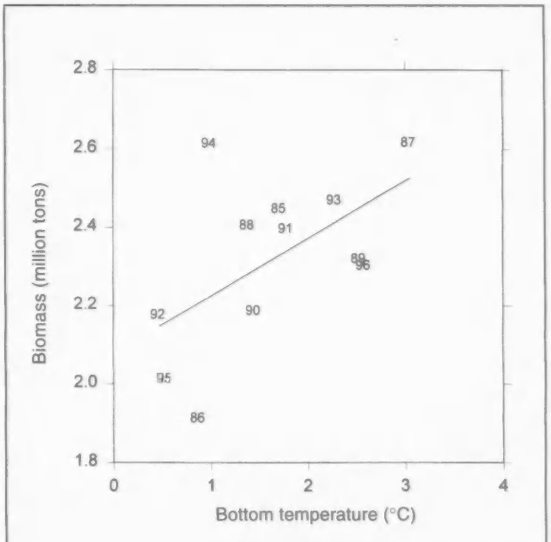

Figure 9

Increase in estimates of yellowfin sole (*Pleuronectes asper*) biomass as related to mean midshelf (50–100 m) bottom temperatures for years 1985–1995. Line represents the linear regression of biomass (dependent variable) against bottom temperature (independent variable); $r^2 = 0.32$, $n = 12$, slope = 0.15 (two-tailed P=0.054), intercept = 2.08. Note that 1982–84 data were excluded because the population structure was unique during those years.

retreat determines the timing of inshore yellowfin sole migration (Bakkala, 1981), and subsequently the timing of spawning, distribution patterns at the time of the survey could be affected. Increasing percentages of spent yellowfin sole during the June 1993 AFSC survey (Nichol, 1995) indicated that spawning activity progresses within the duration of the survey. Spring–summer surveys conducted in warmer years may intercept higher proportions of spent individuals that no longer inhabit the unavailable nearshore spawning areas.

Interannual variation of yellowfin sole biomass estimates within the eastern Bering Sea may be reduced under alternative survey designs (McAllister, 1995). I recommend the incorporation of additional standard stations in nearshore areas, such as the exploratory tows made in Togiak and Kuskokwim Bays (Fig. 2), and east of Nunivak Island. The addition of such stations would likely reduce interannual variation of survey biomass estimates as well as provide a more accurate representation of the population sex-composition.

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Age, growth, mortality, and population characteristics of the Pacific red snapper, *Lutjanus peru*, off the southeast coast of Baja California, Mexico

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Abstract.—Pacific red snapper, *Lutjanus peru*, collected from commercial hook-and-line gear and shrimp trawls off the southeast coast of Baja California Sur, Mexico, were aged by using scales and otoliths (whole-otolith and sectioned-otolith readings). Comparison of ages determined from these structures revealed that scales tend to underestimate ages beyond 5 years, often by more than 1 year, and that they are the least precise structures for ageing. Sectioned otoliths gave greater estimates of age than whole-otolith counts (mean differences <1 yr) and were the most precise structure. The von Bertalanffy growth function described *L. peru* growth satisfactorily with length-at-age determined from whole otoliths and sectioned otoliths. Parameters for the entire population were L_∞ = 97.32 cm, K = 0.1111/yr, t_0 = –0.316 yr (n=1180). No significant differences in length-at-age were found between sexes. The largest individual was a 31-year-old 99.2-cm-TL male, constituting a maximum age, and length record for this species. A multiple regression model of whole-otolith age as a function of otolith and fish measurements provided satisfactory results. Total mortality rates were significantly lower for females (Z=0.282/yr) than for males (Z=0.366/yr).

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The Pacific red snapper, *Lutjanus peru* (Nichols and Murphy), known as "huachinango" in Mexico, is distributed throughout the lower Gulf of California to Peru and found in offshore schools over rocky bottoms to depths exceeding 100 m. It is a commercially important species in Mexico as well as in Central and South America (Thomson et al., 1987; Gutiérrez Vargas, 1990; Ramírez Rodríguez and Rodríguez Medrano, 1990).

Lutjanus peru is fished in most Mexican states along the Pacific coast. The highly valued product is generally marketed whole and transported to inland cities, or occasionally exported. Nationwide, it shares a market with its congener, the Gulf of Mexico red snapper *Lutjanus campechanus* Poey. From 1980 to 1988, the reported catches of both species averaged 6556 metric tons (t) per year (SD 1290 t/yr), of which 56% originated in the Pacific.[1] In Baja California Sur, Pacific red snapper is fished on a small artisanal scale; near Cerralvo Island, *L. peru* ranks within the six most important exploited finfishes (Fig. 1) (Ramírez Rodríguez and Rodríguez Medrano, 1990). As is the case with other snappers, juveniles of this species aggregate over soft bottoms where they are caught as bycatch during shrimp trawling activities (Van Der Heiden, 1985; author's personal observations).

Information on the biology of *L. peru* is limited despite its ecological and commercial importance. Gorelova (1979) performed feeding experiments on juvenile *L. peru* caught off the coast of Peru, whereas Ruiz Santos (1983) studied the reproductive biology of the species off the southwest coast of Mexico and Ruiz and Madrid (1992) studied the biology of a parasitic isopod and its effects on *L. peru* hosts off Michoacán. With the exception of Rocha Olivares and Gómez Muñoz (1993), age and growth of the Pacific red snapper have been estimated either from scales in Mexico (Castro, 1981; Ruiz Luna et al., 1985; Aguilar Salazar, 1986) or from length-frequency distributions in Costa Rica (Gutiérrez Vargas, 1990). The use of scales, however, may result in less than accurate age estimates for some

[1] Anuarios Estadísticos de Pesca, Secretaría de Medio Ambiente Recursos Naturales y Pesca. Av. Progreso Núm. 5, Colonia Del Carmen, Coyoacan. Delegación Coyoacan 04110, México, D.F.

species, including systematic underestimations (e.g. Bilton, 1973; O'Gorman et al., 1987; see review by Beamish and McFarlane, 1987, and papers therein).

Because of the lack of reliable information on biological parameters for this commercially important tropical species, this work represents the first comprehensive study of growth and mortality of a *L. peru* population based on otolith age determinations. A comparison of age estimates from whole and sectioned otoliths and from scales is made to assess their relative usefulness. Growth and mortality rates are estimated, and other aspects of the biology are presented for an exploited population of the Pacific red snapper off the southeast coast of Baja California Sur.

Materials and methods

Study area and sampling scheme

This study took place in Bahía de La Paz, one of two major bays in the Gulf of California (Walker, 1960). The most important fishing grounds for *L. peru* lie within and southeast of the Bay, around Espíritu Santo-Partida and Cerralvo Islands (Fig. 1). Peak catches occur during the summer.

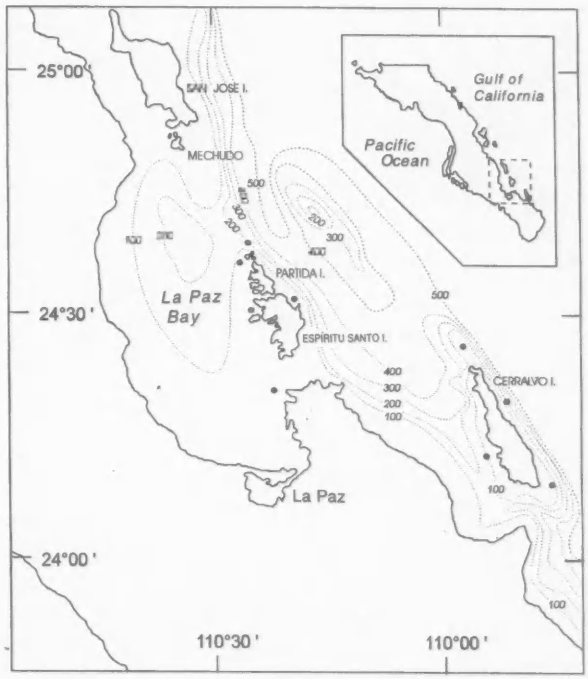

Figure 1

Map of study area showing approximate positions (•) of fishing grounds and sampling sites of Pacific red snapper *Lutjanus peru*. Depth contours are in fathoms.

Pacific red snapper were collected from March 1989 to March 1991. Most samples came from La Paz City fish market, which was sampled at least weekly, March 1989 to February 1991. Snappers were also collected monthly with baited hook and line, May 1989 to February 1991. Juvenile red snappers were collected as shrimp trawler bycatch during February and March 1991. Biological samples were taken from all fish collected (n=2605). In the market, sampling time was limited to the period before fish were stored, therefore biological sampling was restricted to the first 20 randomly selected individuals from each 4-cm length interval. Biological samples consisted of both sagittae, at least 10 scales from underneath the left pectoral fin, and testes and ovaries, which were fixed in 10% buffered formalin and used for sex determination and reproduction studies. Total and standard lengths (TL and SL, respectively) were measured to the nearest mm; total and gutted weights (TW and GW, respectively) were recorded to the nearest 2 or 5 g, depending on fish size. Since fish were gutted on landing, some data and samples could not be obtained from the market. However, many gutted fishes could be sexed from gonadal remains. In 1989, when samples were most abundant, 3085 additional fishes were measured to construct sex-specific length-frequency distributions.

Sample processing and age determination

Because the left and right sagittae did not differ morphometrically[2] or in weight (paired t-tests, P>0.5) in a random subsample of 50 fishes representative of the length range available and since no differences were found in their marking pattern or number of rings, the right otolith was used for age determination when available. Otoliths were submerged in 90% glycerol for 24 hours before they were viewed under a dissecting scope with reflected light over a darkened background. Otoliths embedded in thermoplastic cement were sectioned with a low-speed saw. Three sections (0.3 mm thick), including the primordium and the flanking regions, were made orthogonal to the anteroposterior axis of the structure. Sections were glued to glass slides with cyanoacrylate-based cement and prepared for observation as de-

[2] Measurements compared are those described in Rocha Olivares and Gomez Muñoz (1993).

scribed for whole otoliths. Scales were mounted intact between two glass slides and observed under a dissecting microscope at different magnifications with transmitted light.

Organisms were aged by counting the number of growth marks found in scales (scale age), whole otoliths (whole-otolith age), and sectioned otoliths (sectioned-otolith age). Because a large number of fishes occurred within a restricted length range (Fig. 2), age estimates for whole-otolith ring counts were made on 50 randomly subsampled otoliths from each 2-cm fish-length interval (n=1356) (FAO, 1982). After whole-otolith age determinations were made, a stratified random subsample of these otoliths was sectioned (n=151) and the corresponding scales were used for ageing (10 per fish). Only nonregenerated scales were used for age determinations.

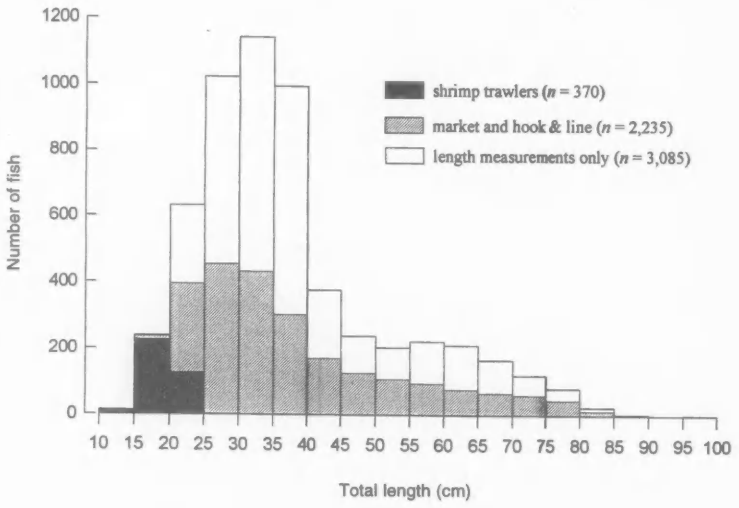

Figure 2

Length-frequency distribution of *Lutjanus peru* collected by hook-and-line and shrimp trawling activities in the southeast coast of Baja California Sur, Mexico. Only fishes from trawls, hook and line, and the market were used for the ageing study.

Two independent whole-otolith age determinations were made at different times by two readers. A third estimate was then made three months later for those otoliths with different ages. Lack of consensus resulted in the otolith being discarded as "noninterpretable," and excluded from the growth analysis. An effort was made to note the cause for rejection. Sectioned otoliths and scales were subject to two reading rounds by one reader separated by a three-month interval.

Estimates of the precision (variation between different reading rounds for each structure) and of the corroboration (variation among structures) were assessed by comparing the percentage of discordant determinations between two data sets (%D) and the index of average percent error of Beamish and Fournier (%E) (1981).

Following the method proposed by Boehlert (1985) of using objective criteria and multiple regression models to determine fish age from otolith measurable parameters, an effort was made to predict Pacific red snapper whole-otolith age by using otoliths and fish morphometrics. This method, originally conceived to save time and costs as well as to reduce the subjectivity involved in otolith reading, was implemented on *L. peru* data and the resulting model used to determine the age of fishes whose otoliths could not be read. Independent variables included otolith weight (to the nearest mg), width, length, ventral radius, anterior radius, fish TL, GW, their logarithmic transformations and squared terms, and a modified condition factor K (gutted weight/ TL^3). Data from a stratified random subsample (FAO, 1982) from the whole-otolith age determinations were used for this analysis (n=285). A stepwise procedure with an inclusion level of P=0.05 was used to select variables for the model. Homoscedasticity and normality were evaluated by residual analysis (Zar, 1984).

Growth

Individual length-at-age (whole-otolith and sectioned-otolith) data were used to fit the von Bertalanffy growth function (VBGF):

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right)$$

where L_t = length at age t;
L_∞ = asymptotic length;
K = growth coefficient; and
t_0 = age at which fish length would be zero if it grows according to the model.

Hotelling's T^2 test (Bernard, 1981) was used to compare growth parameters.

Observed length-at-age data were obtained from whole-otolith readings for most fishes (n=1170) and from sectioned-otolith readings for the largest specimens (n=10). To correct for within-year growth, ages were assigned as follows. Since translucent margin deposition on the otolith peaks in July (Rocha Olivares and Gomez Muñoz, 1993; Fig. 3), only fishes caught during this month were assigned integer ages. For the rest, subsequent growth was accounted for by assigning fractional ages in proportion to the elapsed time (e.g. a fish with two annuli caught in January was assigned 2.5 years).

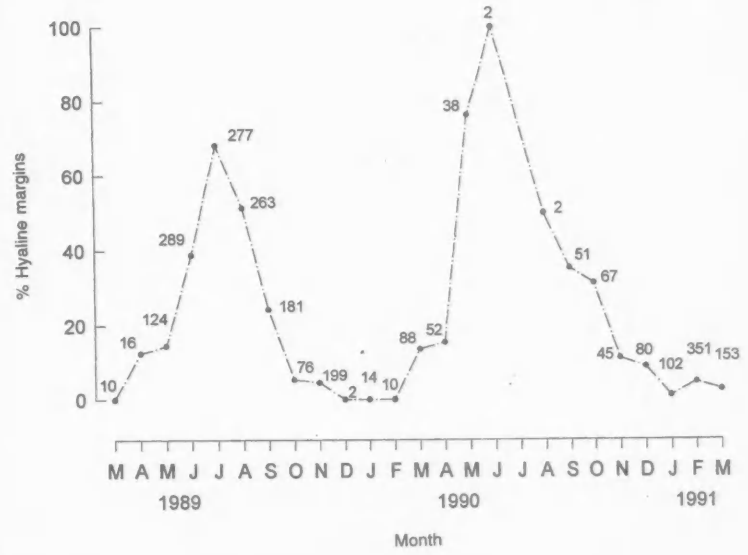

Figure 3

Percentage of translucent margins of the whole otoliths of *Lutjanus peru*. Sample sizes are shown next to symbols.

Length–weight relationships were fitted to the data and used to calculate the von Bertalanffy asymptotic weight (W_∞). Growth performance $\phi = \log_{10}(K) + 2/3 \log_{10}(W_\infty)$ was computed from the growth parameters (Manooch, 1987).

All coefficients of determination reported for nonlinear models were computed by using the following expression (Draper and Smith, 1981):

$$R^2 = 1 - \frac{\sum (y - \hat{y})^2}{\sum (y - \bar{y})^2},$$

where y = observed values;
$\hat{y}$ = predicted values; and
$\bar{y}$ = mean values.

Mortality

An age-length key was constructed from whole-otolith ages for the sexes combined and applied to the length-frequency distributions to construct population age distributions by sex. Total mortality rate (Z) was determined from the descending limb of the resulting catch curves for males, females, and pooled sexes. Hoenig's (1983) combined regression equation was used to obtain another estimate of Z. Owing to the lack of data concerning fishing effort and the unavailability of unfished areas, no direct estimation of the natural mortality rate (M) was possible. Instead, empirical relationships between M and K were used to obtain approximate estimates (Pauly, 1980; Ralston, 1987). A mean bottom temperature of 14°C was assumed for calculating M. This temperature prevails throughout most of the Gulf at depths between 100 and 300 m (Maluf, 1983).

Results

Population parameters and morphometric relations

During the sampling period *L. peru* abundance was variable, and in some months (e.g. March and December 1989 and July to August 1990), sample size was small because of limited supply. Sex determination was possible for only 13.1% of the specimens used for length-frequency distributions (males:females= 1:0.84; H_0=1:1 ratio, χ^2_c=2.85, P=0.091). In the biological sampling, the sex ratio was 1:0.85 (H_0=1:1 ratio, χ^2_c=5.36, P=0.021), indicating that no bias was introduced in the length-frequency sampling with only gonad fragments.

Macroscopic gonad differentiation occurs in *L. peru* between 30 and 35 cm TL (Table 1). A significant fraction of the catch included individuals smaller than 50 cm TL (38% of a total of 2171 kg of gutted fish).

Table 1

Total length composition (cm) of the biological sample of Pacific red snapper by sex. The column labeled "unsexed" groups fishes with undifferentiated gonads (almost all of those <30 cm) and those gutted and with no traces of gonadal tissue (most of those between 30 and 40 cm and all of those > 40 cm).

Size range	Males	Females	Unsexed	Total
10.1–15.0	0	0	24	24
15.1–20.0	0	0	259	259
20.1–25.0	4	5	366	375
25.1–30.0	23	23	404	450
30.1–35.0	67	59	305	431
35.1–40.0	109	76	117	302
40.1–45.0	66	46	59	171
45.1–50.0	40	28	56	124
50.1–55.0	32	24	52	108
55.1–60.0	37	17	38	92
60.1–65.0	26	25	26	77
65.1–70.0	26	23	18	67
70.1–75.0	21	29	11	61
75.1–80.0	9	30	7	46
80.1–85.0	5	9	0	14
85.1–90.0	0	3	0	3
90.1–95.0	0	0	0	0
95.1–100.0	1	0	0	1
Total	466	397	1742	2605

Male and female length compositions were significantly different (Kolmogorov-Smirnov two-sample test, D=0.0836, $0.01<P<0.05$). Although the largest specimen was a 99.2-cm-TL male (Table I), females predominated beyond 70 cm (sex ratio 1:1.97).

Conversion equations for lengths (cm) and weights (kg) did not differ between sexes (ANCOVA, $P>0.05$); therefore data were pooled:

$TL=1.246SL + 0.104$ (n=2603, r^2=0.997, $P<0.001$)

$TW=1.207GW - 0.020$ (n=841, r^2=0.988, $P<0.001$)

$GW=1.763 \times 10^{-5}\ TL^{2.877}$ (n=2350, R^2=0.990, $P<0.001$)

$TW=1.816 \times 10^{-5}\ TL^{2.905}$ (n=844, R^2=0.980, $P<0.001$).

Exponents of the length-weight relationships were significantly different from three (t-test, $P<0.05$).

Age determination

Concentric annuli and circuli were observed in most otoliths and scales. Most scales were found to be interpretable, although circuli were never as clearly defined as otolith annuli. Most samples (n=92) presented less than 40% regenerated scales. A correlation was found between the percentage of regenerated scales and fish length (r=0.310, $P<0.001$).

Table 2

Values of percent disagreement (%D) and percent average error (%E) for whole-otolith, sectioned-otolith, and scale age determinations for individual structures (precision) and between the structure and whole-otolith age (between structures) of Pacific red snapper. No. = number of determinations. Rejections are otoliths not included in the analysis for being too large (size) or for lacking a clear marking pattern (other).

	Index		Rejections		
Age	%D	%E	No.	Size	Other
Precision					
Whole-otoligh	16.90	3.89	143	7	1
Sectioned-otolith	10.42	2.13	144	1	6
Scale	34.01	4.19	147	2	2
Between structures					
Sectioned-otolith	26.36	2.82	129		
Scale	58.65	8.86	133		

Of the 1356 otoliths used for whole-otolith age determinations, 186 were discarded for the following reasons: large size prevented the enumeration of all the growth rings (2.2%), breakage or loss (1.4%), deformities or abnormal calcification (2.3%), and non interpretable otoliths as defined in the "Methods" section (7.8%). Whole-otolith ages were available for 1170 individuals ranging from 10.2 to 83.5 cm TL.

A number of scales and otoliths were also rejected in the comparison of whole-otolith, sectioned-otolith, and scale ages (Table 2). Noninterpretable otoliths were included in the computation of precision indices, but not in the between-structures indices. Most of the rejections of whole otoliths were due to size, but a similar proportion of sectioned otoliths lacked a clear marking pattern. Sectioned otoliths and scales were the most and least precise structures, respectively, for age determination (Table 2). The %D indicates a factor of three difference in the precision of sectioned otoliths and scales. However, the %E shows that such differences are less important (less than a factor of two) because this index incorporates the difference in age estimations (Beamish and Fournier, 1981). The difference between whole-otolith ages and sectioned-otolith or scale ages was much larger (Fig. 4). Sectioned-otolith ages were found to be at least twice as similar to whole-otolith ages as scale ages according to %D, and more than three times as similar according to %E (Table 2).

The magnitude of the discrepancies in age determinations among structures increased with both age and length of the fish (Fig. 4). Differences between scale

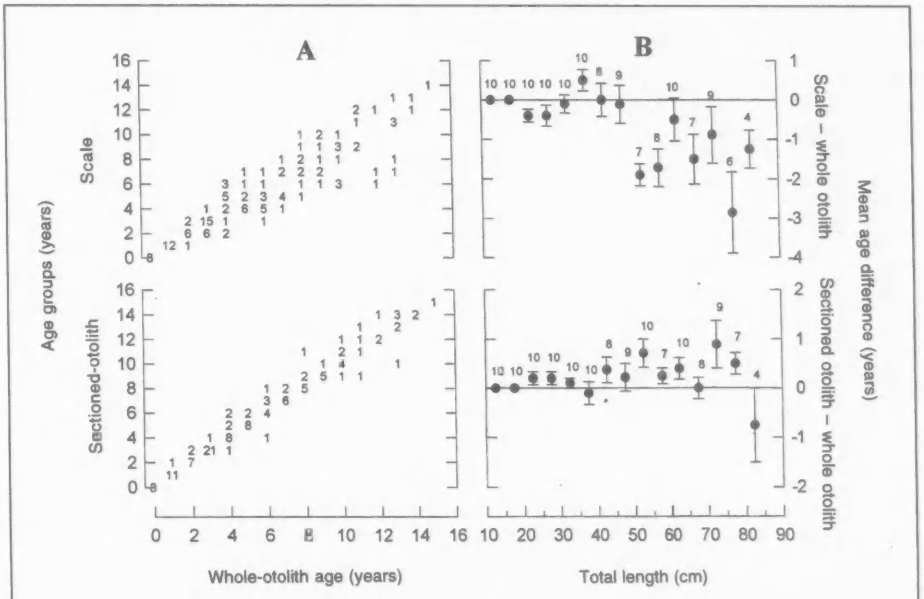

Figure 4

(**A**) Scatter plots of sectioned-otolith and scale ages against whole-otolith ages. Numbers represent the frequency of occurrence. (**B**) Mean age difference (± standard error of the mean) of scale and sectioned-otolith ages minus whole-otolith age against length of *Lutjanus peru*.

and whole-otolith ages were as large as six years, whereas for sectioned otoliths, differences did not exceed three years (Fig. 4A). Scale ages were consistently lower than whole-otolith ages in fish larger than 50 cm TL, whereas the largest sectioned-otolith and whole-otolith age deviations were found in fish above 40 cm TL (Fig. 4B). The mean sectioned-otolith and whole-otolith age deviations did not exceed one year, although mean scale and whole-otolith age deviations often exceeded one year.

Six independent variables with highly significant coefficients were included in the multiple regression model (Table 3). The model explained 96% of the variability in the data with a standard error of less than one year. A linear regression of whole-otolith age on otolith weight alone accounted for 93% of the variance. The residuals revealed a trend indicating a certain degree of heteroscedasticity but were normally distributed (χ^2=10.41, P=0.005). Whole-otolith ages determined with the multiple regression model for 28 fish with unreadable otoliths were very close to the VBGF (see "Discussion" section).

Table 3

Regression coefficients for the multiple regression model of whole-otolith age as a function of otolith and fish measurements of Pacific red snapper. SE = coefficient standard error, SEE = standard error of the estimate. R = multiple correlation coefficient; No. = number of observations.

Variable	Coefficients	SE	P
Intercept (c)	–6.183	1.0940	0.000
Total length squared	1.306E-03	1.4910E-04	0.000
ln(Gutted weight)	1.353E-05	3.1700E-06	0.000
Otolith weight squared	5.915	0.7313	0.000
Otolith width squared	–7.391E-01	2.4400E-01	0.000
ln (otolith ventral radius)	2.153E-02	7.6050E-03	0.005
Otolith weight	–1.014E-02	3.3360E-03	0.003
		R =	0.9797
		SEE =	0.6469
		No. =	283

Growth

Mean observed length-at-age were not significantly different between sexes, (t-tests, 0.95>P>0.09), however male and female VBGF parameters computed separately from individual data were significantly different (T^2=609.5, P<<0.001) (Fig. 5). The 99% Roy-Bose simultaneous confidence intervals indicated that the three VBGF parameters significantly contributed to the observed difference in predicted growth ($6.091 \leq L_\infty$

(male) – L_∞(female) ≤ 8.419, –0.026 ≤ K(male) – K(female) ≤ –0.020, –0.511 ≤ t_0(male) – t_0(female) ≤ –0.344).

Of the thirty otoliths too large for whole-otolith reading, ten were randomly selected, sectioned, and read, yielding ages of 15 years and above. The VBGF parameters computed from all available data, including whole-otolith and sectioned-otolith ages (n=1180) were considered to be representative of the population (asymptotic standard error): L_∞ = 97.32 cm (1.816), K = 0.1111/yr (4.073 × 10^{-3}), t_0 = –0.316 (0.0569) (n=1180, R^2=0.93). The asymptotic length was converted to an asymptotic weight of W_∞ = 10.84 kg. The growth performance of *L. peru* was ϕ = 1.736. The age composition of the sampled males differed significantly from that of the females (Kolmogorov-Smirnov two-sample test, D=0.0843, 0.01<P< 0.05) (Fig. 6).

Mortality

The length range of most age groups was on the order of 20 cm (Table 4: Fig. 7A). Catch curves were constructed for males, females, and pooled sexes. Total mortality rates (Z) were calculated without the extreme age groups and those not fully recruited to the fishery (Fig. 8). Total instantaneous mortality rate for females, estimated from the catch curves, was significantly lower compared with those for males (t=–2.112, df=52, P<<0.001). Hoenig's formula should be applied to the maximum age of "the largest few fish" (Hoenig, 1983). On the basis of this recommendation and the fact that only one out of 5690 fishes measured in this study was larger than 90 cm, this 31-year-old fish was interpreted as an outlier and a t_{max} = 26 years was considered more representative of the population. This value yielded a Z = 0.172/yr, which is considerably lower than the catch curve estimates. The estimates of M obtained from the empirical relationships 0.222/yr (Pauly, 1980) and 0.248/yr (Ralston, 1987) were compatible with the catch curve mortality estimates giving exploitation rates F/Z) ranging from 0.121 (females) to 0.393 (males).

Discussion

Sampled length range

The accurate estimation of growth parameters depends, among other factors, on the adequate sampling of the length range of a species. The fish used in this study covered most of the known length range of the Pacific

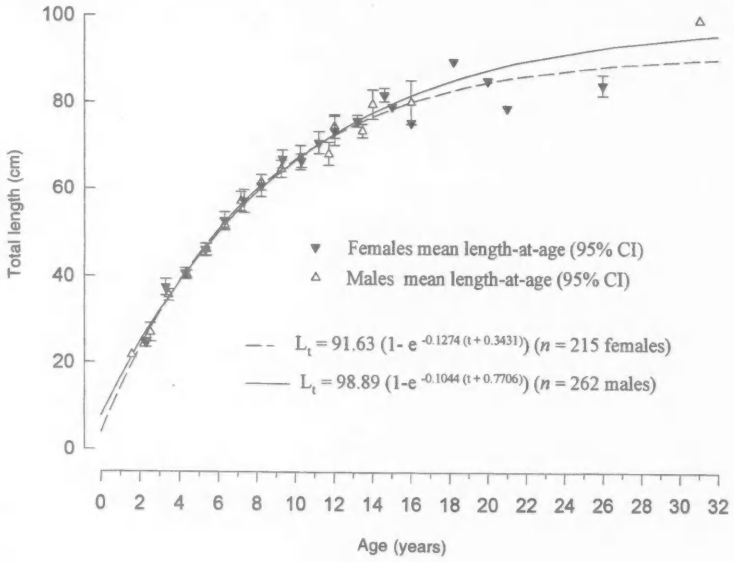
Total length (cm)
100
80
60
40
20
0
0 2 4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
Age (years)
Females mean length-at-age (95% CI)
Males mean length-at-age (95% CI)
$L_t = 91.63\ (1 - e^{-0.1274\ (t + 0.3431)})$ (n = 215 females)
$L_t = 98.89\ (1 - e^{-0.1044\ (t + 0.7706)})$ (n = 262 males)

Figure 5

Fitted VBGF curves and mean length-at-age (whole-otolith and sectioned-otolith) for *L. peru* females (dashed line, filled triangles) and males (solid line, open triangles). 95% CIs are shown.

red snapper (10 to ca. 100 cm TL). The lower size limit of *L. peru* in the hook-and-line catch (18.3 cm) was very close to that reported for *L. campechanus* fished with similar size hooks in the Gulf of Mexico (18.0 cm) (Nelson and Manooch, 1982). This might indicate a comparable vulnerability due to morphological similarity. Because fishermen do not typically change hook size to target small snappers (personal observation), the preponderance of small fish in the catch (ca. 61% in numbers) that had not yet recruited to the spawning population was not due to gear selectivity. The upper limit of the range was also sampled and a length record is reported for the species. Thus it seems unlikely that the growth parameters of *L. peru* may be biased owing to inadequate sampling of its length-range.

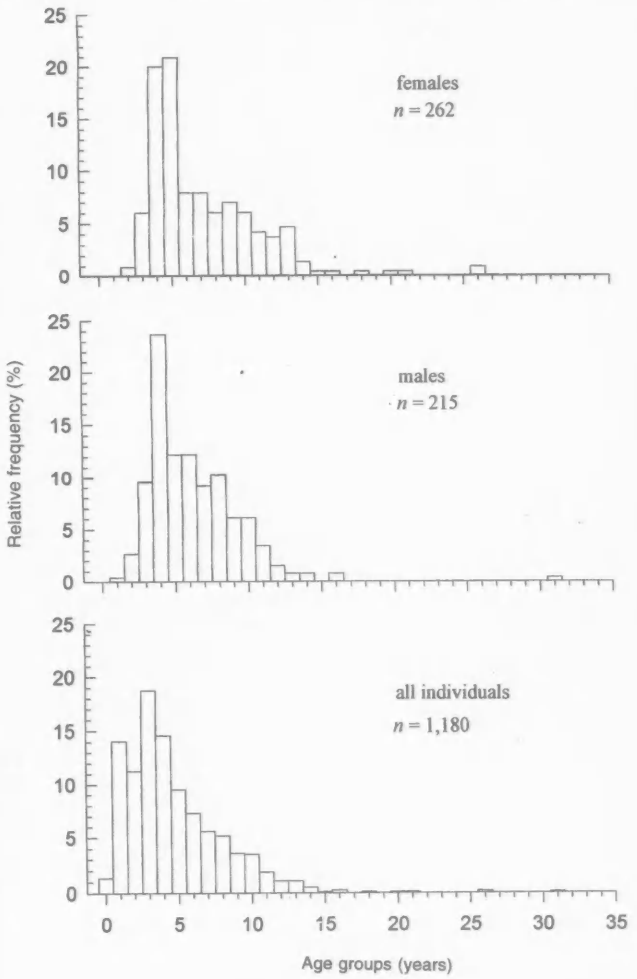

Figure 6

Age structure of *Lutjanus peru* females, males, and sexes combined of directly aged specimens collected at La Paz fish market or caught by hook-and-line and shrimp trawling activities off the southeast coast of Baja California Sur. Data represent whole-otolith ages (up to 15 years) and sectioned-otolith ages (beyond 15 years). Most of the unsexed individuals are undifferentiated fish but some are reproductively active adults that could not be sexed.

Age determination

The monthly fluctuation in the percentage of translucent margins suggests that the period of translucent ring formation takes place in the summer during the spawning season (Fig. 3). This observation enabled Rocha Olivares and Gómez Muñoz (1993) to indirectly validate whole-otolith rings as annuli in *L. peru* up to 10 years old.

The greater precision of sectioned otoliths suggested by %D and %E resulted from a more direct access to the marking patterns of the structure. Different degrees of wear and tear were noted on the anterior margin of large scales, which contributed to age determination variability within reading rounds. Comparison of individual age estimates of *L. peru* from whole otoliths, sectioned otoliths, and scales provided evidence supporting age underestimation by the latter. This underestimation by scales has also been observed in the Antarctic fish *Notothenia gibberifrons* Lonnberg (Coggan et al., 1990). Libby (1985) also concluded that whole-otolith ages were more accurate and less subjective than scales for ageing the anadromous alewife, *Alosa pseudoharengus* (Wilson). As in other species, however, this effect does not seem to be very important during the first five years in *L. peru*. For example, Lou (1992) found that either scales or sectioned otoliths provided reliable age estimates up to five years in the tropical parrotfish *Scarus schlegeli* (Bleeker), and Lowerre-Barbieri et al. (1994) reported similar findings in weakfish, *Cynoscion regalis* (Bloch and Schneider), to age six. Apparently, otoliths are more reliable structures than scales (Beamish and McFarlane, 1987) over most ages, and this study extends this observation to the Pacific red snapper.

A number of studies have compared whole and sectioned otoliths as alternative structures for age determination. The magnitude of the difference between whole-otolith and sectioned-otolith age varies from species to species, but the general trend is an underestimation of whole-otolith ages in older fishes. Wilson and Boehlert (1990) found that sectioned-otolith ages produced smaller L_∞ estimates than whole-otolith ages, but growth rates were similar for both in the canary rockfish, *Sebastes pinniger* (Gill). In the long-lived orange roughy, *Hoplostethus atlanticus* Collett, Smith et al. (1995) found that sectioned-otolith ages exceeded whole-otolith ages after the age of reproductive maturity. Ferreira and Russ (1994) found in the Great Barrier reef coral trout, *Plectropomus leopardus* (Lacépède), that the mean difference between sectioned-otolith and whole-otolith readings remains within one year in fishes up to 12 years, but increases abruptly to almost four years for age groups 13 and 14. Pearson et al. (1991) found that whole-otolith ages tend to be as much as eight years less than broken-and-burnt otolith ages in the shortbelly rockfish, *S. jordani* Gilbert. In *L. peru*, discrepancies between whole-otolith and sectioned-otolith ages were not extreme, but whole-otolith age determinations were not reliable beyond the 15th annulus. It would be useful to extend these observations to other populations of *L. peru* to assess the variability of this pattern.

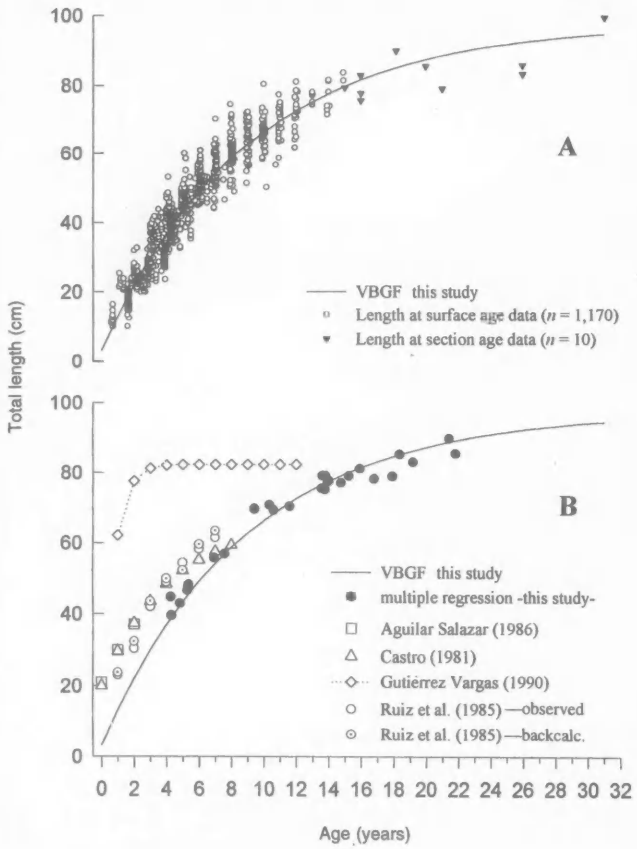

Figure 7

(**A**) Scatter plot of all length-at-age data used for VBGF parameter estimation. Length-at-whole-otolith age (circles), length-at-sectioned-otolith age (triangles), and VBGF curve obtained from this study (solid line). (**B**) VBGF curve from this study (solid line) and lengths at age reported in other studies of age and growth of *Lutjanus peru*. Mean observed lengths at age (open circles) and mean back-calculated (dotted open circles) from Ruiz et al. (1985); mean observed length at age from Aguilar Salazar (1986) (squares), mean observed length at age from Castro (1981) (triangles). Diamonds joined by a dotted line indicate the von Bertalanffy growth curve reported by Gutiérrez Vargas (1990). Filled circles represent age estimates obtained with the multiple regression model for "unreadable" otoliths.

The coefficient of determination of the multiple regression model is affected by the degree of colinearity of the independent variables. Although not all the assumptions required for the use of a multiple regression model are met by the data set, including homoscedasticity, this does not preclude its results to serve as a first-order age approximation. Otolith weight appears to be a very good predictor of age in this species, as it has been observed in *P. leopardus* (Ferreira and Russ, 1994). The model was used to estimate the age of those otoliths that had been discarded as unreadable and for which all variables were available, placing the predicted ages very close to the VBGF curve (Fig. 7B). The success of this method suggests that it could be implemented for routine age determination of this species.

Growth

The growth of *L. peru* was satisfactorily described by the generalized VBGF. The absence of a significant difference in mean length-at-age between sexes and the significantly different growth parameters might seem contradictory. However, the graphic representation of the data revealed that both sexes have very similar growth schedules during

the first 10–12 years (Fig. 5). The very few males sampled beyond the ascending limb of the curve may have prevented a more constrained curve fit in this region.

The results of this and other studies made in Mexico and Costa Rica reveal the following patterns: 1) scale-based studies, using traditional methods for growth parameter estimation, yield higher growth rates resulting from age underestimation if large fishes are involved (Table 5, reference A) but not so if only small fishes are included (Table 5, reference B); 2) small asymptotic lengths may result from a restricted length range (Fig. 7B); 3) length-frequency based methods for growth parameter estimation yield fewer age classes and unrealistic growth rates, which have been observed elsewhere (Grimes, 1987; see also Rocha Olivares, 1991, for examples of unpublished data). It is possible that part of the observed differences in the growth parameters of *L. peru* between peninsular and continental populations are "true"; however the diversity of fishing gears and selectivities used in different states (Aguilar Salazar, 1986) and the poor effort invested in systematic biological data collection make interpopulation comparisons difficult.

The presence of an individual of ca. 100-cm TL represents a length record for the species. The sectioned-otolith age of this fish (31 years) also constitutes a record for the maximum age of an eastern Pacific lutjanid, and adds *L. peru* to the list of long-lived snappers (i.e. exceeding 30 years of age): *L. bohar* (38 years), *L. adetti* (37 years), *L. sebae* (35 years) (Loubens, 1980), *L. malabaricus* (46 years) (Mathews and Samuels, 1985), and *L. quinquelineatus* (32 years) (Newman et al., 1996). When compared with the growth trends observed in the family, growth performance of *L. peru* (ϕ=1.74) falls above the mean value for lutjanids (1.65) but within the expected range (1.08–2.15; SD=0.35) (Munro, 1983). Furthermore, the combination of L_∞ = 97.32 cm and K = 0.1111/yr of the Baja California population of Pacific red snapper is very close to the functional relationship of $\log_{10}(K)$ versus $\log_{10}(L_\infty)$ reported by Manooch (1987) for snappers (Lutjanidae) and groupers (Serranidae).

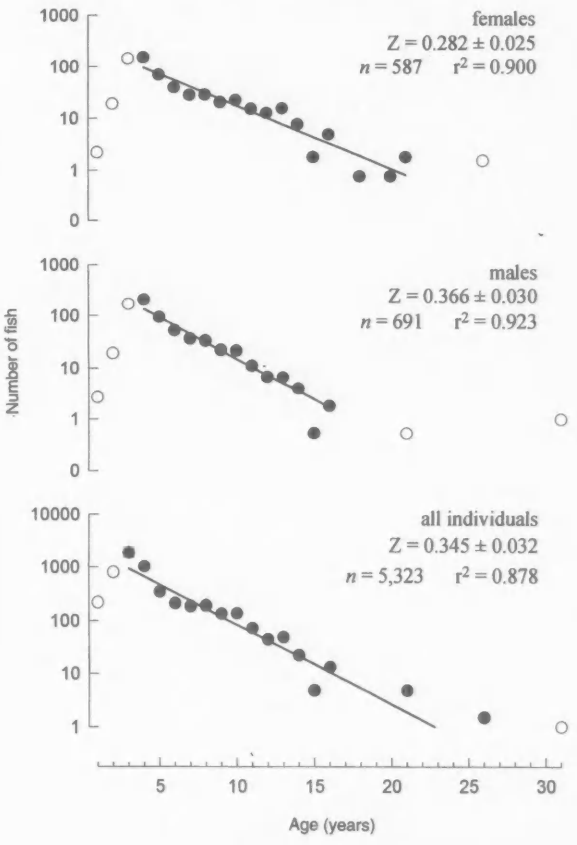

Figure 8

Catch curves and estimates of total mortality of *Lutjanus peru* females, males and sexes combined, caught by hook and line off the southeast coast of Baja California Sur. The age composition was computed with an age-length key and the length composition of the massive and biological samples. Total mortality rates Z (per year ± standard error) are presented for females, males, and the entire population. Black dots represent data points included in the calculation of the slope (solid line).

Mortality

In this study, estimates of M were restricted to the use of empirical relationships between M and K because no effort data were available and no unfished areas could be sampled. It has been repeatedly observed that these two parameters are inversely related across a large number of fish taxa (Pauly, 1980). Hoenig's (1983) empirical formula yielded an unrealistically low estimate of mortality, as it probably would in other long-lived snappers. When compared to total mortality rates (Z), estimates of M are consistent and yield much lower exploitation rates and F/M ratios than those reported for other lutjanids (cf. Table 8.2 in Ralston, 1987), probably as the result of an overestimation of M by the empirical formulae.

Male predominance in population sex ratios is not uncommon among lutjanids (cf.

Table 5.1 in Grimes, 1987). Populations of *L. peru* studied in Baja California Sur and Michoacán off continental Mexico show this bias (1:0.82, n=785; Ruiz Luna et al., 1985). In lutjanids, evidence suggests that skewed sex ratios probably reflect differential growth and mortality between sexes (Grimes, 1987). Other reproduction studies on lujanids have also suggested a tendency for females to be more common at larger sizes. The population sampled in this study shows significant differences in mortality rates

Table 4

Age-length key used in the construction of the catch curves of Pacific red snapper, *L. peru*. Ages represent whole-otolith ages except for fish older than 15 years for which sectioned otoliths were used.

Length	Age group (year)																				
Group (cm)	0+	1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+	13+	14+	15+	16+	18+	20+	21+	26+	31+	Total
10.1–15.0	15	8																					23
15.1–20.0	1	107	2																				110
20.1–25.0		50	69	8																			127
25.1–30.0		1	58	62																			121
30.1–35.0			4	102	17																		123
35.1–40.0				40	70	7																	117
40.1–45.0				9	67	37	2																115
45.1–50.0					17	53	26	2	1														99
50.1–55.0					1	9	47	26	6		1												90
55.1–60.0						6	8	24	23	10	3												74
60.1–65.0							3	11	20	9	11	3	1										58
65.1–70.0								1	6	17	20	7											51
70.1–75.0								2	5	6	4	10	8	7	1								43
75.1–80.0											1	2	3	6	1	1	2			1			17
80.1–85.0											1		1		4		1						7
85.1–90.0																		1	1		2		4
> 90																						1	1
Total	16	166	133	221	172	112	86	66	61	42	41	22	13	13	6	1	3	1	1	1	2	1	1180

Table 5

Comparison of growth parameters of *Lutjanus peru* obtained in studies from Mexico and Costa Rica (F-W=Ford-Walford plot, NL=nonlinear regression, n=sample size, LFA=length-frequency analysis, obs=observed lengths, back=back-calculated lengths, NA=not applicable).

	Reference					
	A		B	C	D	E
Study site	Michoacan		Michoacan Guerrero Oaxaca	Baja California Sur (Los Cabos region)	NW Costa Rica	Baja California Sur (Bahía de La Paz region)
Structure used	scales		scales	scales	NA	otoliths
Method	F-W		F-W	F-W	LFA	NL
Data	obs.	back	obs.	back	NA	obs
L_∞ (cm)	81.5	79.5	82.64	66.71	83.34	92.85
K (per yr)	0.196	0.191	0.11	0.23	1.46	0.12
t_0 (yr)	0.725	0.786	1.48	–0.54	0.04	0.14
n	1068	412	175	208	5902	1180
Age range (yr)	1–7	1–7	0–2	0–8	1–12	0–31
Size range (cm)	23–62	24–64	21–37	20–59	24–82	10–99

A = Ruiz et al. (1985); B = Aguilar Salazar (1986); C = Castro (1981); D = Gutierrez Vargas (1990); and E = this study.

between sexes. The higher mortality rate of males may account for the biased sex ratio. In no other lutjanid species has such a large difference in total mortality been observed between males and females. Whether this difference results from different availability to the fishing gear, spatial segregation, or foraging behaviors (F-associated difference), or from differences in predator vulnerability or natural longevity (M-associated difference) requires further research.

In this paper I have compared the merit of scales, whole otoliths, and sectioned otoliths to age the Pacific red snapper, *L. peru*. As is the case for other tropical and semitropical fishes, the usefulness of whole-otolith age determination is limited up to a certain age, after which, sectioned otoliths are the only reliable method for ageing and scales should be avoided. Age determinations from whole and sectioned otoliths of fishes covering most of the known size range of *L. peru* were used to determine the VBGF parameters. A 31-year-old fish measuring 99.2 cm is reported and constitutes a record size and age. Total mortality rates were higher for males resulting in a preponderance of females among the older fishes.

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Enhancing diet analyses of piscivorous fishes in the Northwest Atlantic through identification and reconstruction of original prey sizes from ingested remains

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Abstract.—Biological interactions among species can play a dominant role in structuring marine fish communities. Specifically, predation may represent a significant source of mortality for larval and juvenile fishes. Analysis of predator diet requires accurate information on the identity as well as the sizes of prey consumed. In examinations of stomach contents of piscivorous fishes, the condition of recovered prey items varies substantially not only in the large range of digestive states encountered but also in the occurrence of partially consumed fishes. To estimate the original sizes of well-digested and partially consumed prey fishes we constructed a series of predictive equations relating total length, fork length, and weight of fish to seven morphometric measurements including dorsoventral body depth, eye diameter, caudal peduncle depth, pectoral-fin length, opercle length, cleithrum length, and dentary length for ten common prey fishes in the Northwest Atlantic. All relationships were highly significant, with coefficients of determination typically exceeding 0.90 and mean percent prediction errors less than 10%, indicating that reliable original size estimates are obtainable from incomplete fish remains. To aid in field-based identification of prey fishes, we extracted and examined opercles, cleithra, and dentaries from each fish. Careful examination of bones revealed prominent diagnostic characteristics with clear differences among family taxa, demonstrating their potential utility as identification tools. Used collectively, the predictive equations and the diagnostic features of the bones should allow for inclusion in diet analyses of prey items previously designated as unidentifiable or unmeasurable, and thus increase the amount of dietary information obtainable from stomach contents analyses of Northwest Atlantic piscivores.

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Biological interactions among species can significantly affect the dynamics of marine fish populations (Overholtz et al., 1991; Rothschild, 1991). Specifically, predation by piscivorous fishes is recognized as an important mechanism in structuring fish communities (Hackney, 1979; Lyons and Magnuson, 1987; Tonn et al., 1992), particularly in the role it plays to potentially regulate natural mortality rates and recruitment of larval and juvenile fishes (Sissenwine, 1984; Houde, 1987; Bailey and Houde, 1989). In order to estimate consumption rates of key predators, details are needed on the types and sizes of prey fishes consumed across spatial and temporal scales. However, because of the substantial variability in the condition of recovered prey items, the collection of stomach contents data in the field is often limited to only those items that are readily identified and measured, resulting in the loss of potentially important diet information.

Identification of piscine prey ingested by fish, avian, and mammalian predators has frequently involved the use of diagnostic bones including vertebrae (Pikhu and Pikhu, 1970; Feltham and Marquiss, 1989; Carss and Elston, 1996), pharyngeal arches (McIntyre and Ward, 1986; Raven, 1986), opercular bones (Newsome, 1977), the axial skeleton

and hypurals (Trippel and Beamish, 1987), and cleithra and dentaries (Hansel et al., 1988). Measurements of the dimensions of diagnostic bones have often then been used to estimate original prey size (Trippel and Beamish, 1987; Hansel et al., 1988; Carss and Elston, 1996). Previous studies on the food habits of piscivores have used fish otoliths as an aid in prey identification and original prey size estimation (Jobling and Breiby, 1986). However, acidic preservatives, such as formaldehyde, can dissolve otoliths, resulting in unreliable otolith length and fish length relationships (McMahon and Tash, 1979). In addition to bones, external morphological measurements, such as eye diameter and caudal peduncle depth, have been used successfully to reconstruct prey body size for recently consumed prey fishes (Crane et al., 1987; Scharf et al., 1997). However, the majority of fish feeding studies employing such techniques have been directed at freshwater piscivores, whereas researchers examining the diets of marine fishes have utilized these techniques much less frequently (Crane et al., 1987; Scharf et al., 1997). Moreover, no such techniques are currently available to enhance diet analyses and more completely define the role of piscivorous fishes in structuring fish communities in the Northwest Atlantic.[1]

Here, we generate a series of predictive regression equations to estimate prey fish total length, fork length, and weight for ten fish species. Original fish size is estimated from four external morphometric measurements including maximum body depth, eye diameter, caudal peduncle depth, and pectoral-fin length, as well as from length measurements of three diagnostic bones: the opercle, the cleithrum, and the dentary. The prey species used here include several of commercial and recreational importance and commonly occur in the diets of marine piscivores in the Northwest Atlantic, representing approximately 52% of the total fish prey consumed by piscivorous fishes during 1973–90 (Grosslein et al., 1980; Langton and Bowman, 1981).[2] We also identify and describe the unique characteristics of the three diagnostic bones for each fish species and assess their potential value as tools for field identification of prey fishes recovered from predator stomachs.

Materials and methods

Over 700 fish representing ten species in five families ranging in size from 52 to 340 millimeters (mm) total length (TL) were measured and dissected (Table 1). Fish were collected as part of Food Chain Dynamics Investigation (FCDI) (NEFSC, NMFS) research cruises conducted on Georges Bank during June and August of 1995 and 1996. FCDI research cruises were sponsored through the National Oceanic and Atmospheric Administration Coastal Ocean Program-Georges Bank Predation Study. Fish were also collected from waters off the Northeast U.S. coast during September and October of 1996 as part of the NEFSC Fall bottom trawl surveys. Additional fish were collected by personnel from the Massachusetts Division of Marine Fisheries as part of a coastal trawling survey conducted in May and September of 1996. All fish were immediately frozen until they could be returned to the laboratory. In the laboratory, fish were thawed and weighed wet to the near-

[1] Rountree, R. A. 1997. Food Chain Dynamics Investigation (FCDI). Northeast Fisheries Science Center (NEFSC), National Marine Fisheries Service (NMFS), 166 Water St., Woods. Hole, MA 02543. Personal commun.

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Table 1

Family, species, number (n), and size range (total length in millimeters) of prey fishes used to construct predictive equations.

Family	Species	Common name	n	Size range
Clupeidae	*Alosa pseudoharengus*	Alewife	137	73–282
	Alosa aestivalis	Blueback herring	38	83–134
	Clupea harengus	Atlantic herring	84	97–269
Scombridae	*Scomber scombrus*	Atlantic mackerel	56	158–330
Stromateidae	*Peprilus triacanthus*	Butterfish	108	54–193
Ammodytidae	*Ammodytes dubius*	Sand lance	75	109–209
Gadidae	*Urophycis chuss*	Red hake	45	108–340
	Merluccius bilinearis	Silver hake	95	75–300
	Melanogrammus aeglefinus	Haddock	47	79–202
	Gadus morhua	Atlantic cod	31	52–140

est 0.01 gram (g) before external measurements were completed to the nearest 0.01 mm with digital calipers. To remove diagnostic bones, fish were placed in boiling water for 30–90 seconds, depending on fish size. Bones were then extracted from the soft tissue and measured to the nearest 0.025 mm with an ocular micrometer (2.75×).

Least squares regression equations (StataCorp., 1995) were generated to predict original total length, fork length, and weight from measurements of body depth, eye diameter, caudal peduncle depth, pectoral-fin length, opercle length, cleithrum length, and dentary length. The left eye, left pectoral fin, and diagnostic bones from the left side of each fish were used consistently unless damaged. Body depth was measured as the maximum linear dorsoventral distance with fins depressed. Eye diameter was measured horizontally along the anteroposterior axis. Caudal peduncle depth was measured dorsoventrally. Pectoral-fin length was measured from the anterior most point of fin insertion to the tip of the longest fin ray. Opercle length was measured as the maximum linear dorsoventral distance, usually from the dorsal most point to the tip of the primary ray (Fig. 1). Cleithrum length was measured from the tip of the dorsal process to the tip of the ventral process (Fig. 2). Dentary length was defined as the maximum linear anteroposterior distance from the symphyseal margin located anteriorly between the left and right dentaries to the posterior tip of the dorsal or ventral process, whichever was longer (Fig. 3). A series of least squares regression equations to predict fish weight from total or fork length for each species was also generated. To further assess the strength of individual bivariate relationships, mean percent prediction errors (Smith, 1980) were determined for each regression by averaging the percent prediction error calculated for each observation as

$$[(Observed - Predicted) / Predicted] \times 100.$$

Forward and backward stepwise linear regressions (StataCorp., 1995) were performed in an attempt to identify the best set of predictor variables. To ensure that all variables in the stepwise model were individually significant, the value of the F-statistic used to determine variable inclusion was set at four (Draper and Smith, 1981).

Opercles, cleithra, and dentaries were also carefully examined to identify distinguishing characteristics that may be potentially useful for identification of each fish species. Several features of each bone were examined for differences among species, including the general shape of each bone; the numbers and orientation of ridges on the opercle and the curvature of opercle margins; the numbers, sizes, and shapes of cleithrum processes; and the presence or absence of teeth on the dentary, with attention given to overall tooth size, shape, and orientation, as well as the shapes and relative lengths of dentary processes.

Results

Predictive equations

Regressions relating external morphological measurements to total and fork length were all highly significant ($P<0.0001$), with r^2 values ranging from 0.63 to 0.99 and mean percent prediction errors ranging from 2.68 to 10.83 (Table 2). Regressions from measurements of eye diameter to predict original fish length were typically more variable than those from other external measurements. This was likely due to measurement error associated with damage of the soft adipose tissue surrounding the eye incurred during the freezing and thawing processes. Regressions relating diagnostic bone measurements to total and fork length were also highly significant ($P<0.0001$), with r^2 values ranging from 0.81 to 0.99 and mean percent prediction errors ranging from 1.26 to 8.48 (Table 3). Compared with regressions from external morphological measurements, variation in diagnostic bone measurements typically explained more of the variation in original fish length (94% of r^2 values >0.90) and bones were generally more precise in predicting fish length (87% of mean %PEs < 5.00). Stepwise linear regressions indicated that cleithrum length was the most consistent predictor of original fish length and it was included in the best set of predictor variables for 8 of 10 species (Table 4). Pectoral-fin length was included in the best set of predictors for 6 species, whereas dentary length was included for 5 species. The remaining independent variables were included in the best set of predictors for either 3 or 4 species, respectively.

Regressions relating external morphological measurements and diagnostic bone measurements to fish weight were also each highly significant ($P<0.0001$), with r^2 values ranging from 0.71 to 0.99 (Table 5). Mean percent prediction errors for regressions predicting fish weight ranged from 5.97 to 39.17. These were typically higher compared with prediction errors for regressions predicting fish length, indicating that estimates of original fish length were more precise than estimates of original prey weight. Similar to length regressions, diagnostic bone measurements yielded higher r^2 values and lower mean percent prediction errors when regressed against fish weight compared with external morphological mea-

surements. Stepwise linear regressions indicated that body depth, caudal peduncle depth, and cleithrum length were the most consistent predictors of original fish weight and were included in the best set of predictor variables for 8, 9, and 8 species, respectively (Table 6). Pectoral-fin length was included in the best set of predictor variables for 5 species, whereas opercle length was included for 3 species. Dentary length and eye diameter appeared to be the least consistent predictors of fish weight and were included in the best set of predictor variables for 1 and 0 of the species, respectively. Lastly, measurements of total and fork length were significantly related to total weight for each species ($P<0.0001$) with

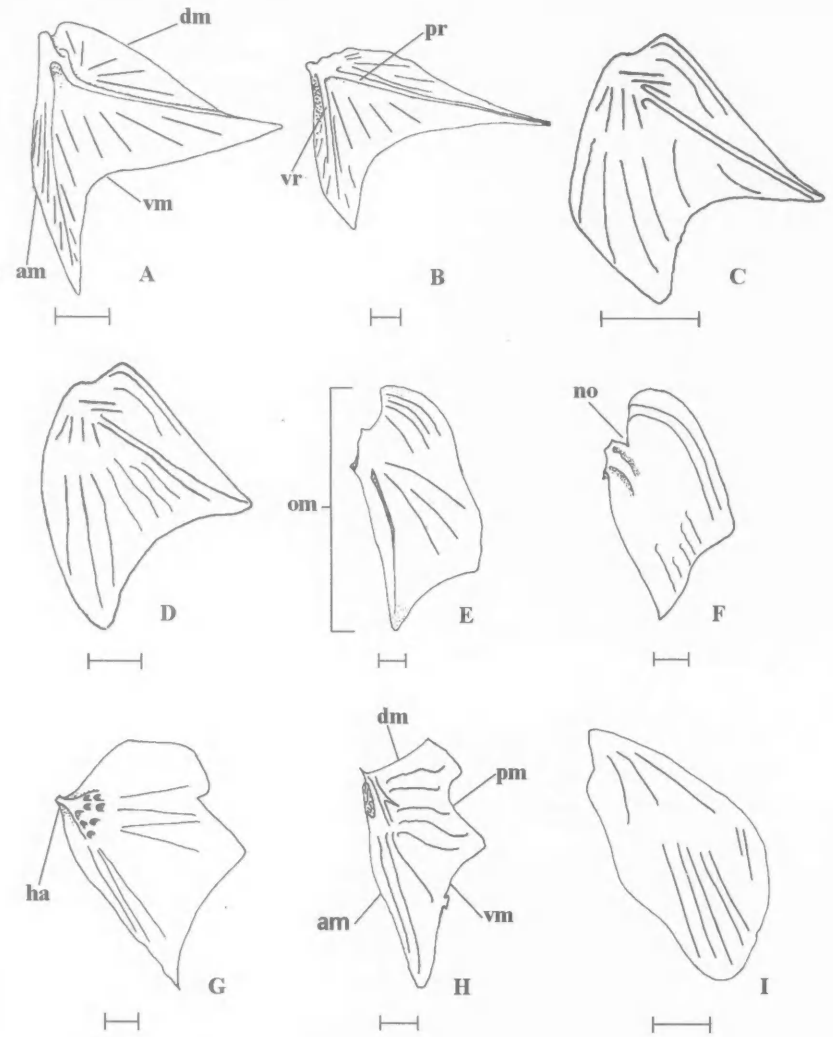

Figure 1

Left opercles from nine species of marine fishes in the Northwest Atlantic: (**A**) silver hake; (**B**) red hake; (**C**) Atlantic cod; (**D**) haddock; (**E**) alewife; (**F**) Atlantic herring; (**G**) Atlantic mackerel; (**H**) butterfish; (**I**) sand lance. Opercles are presented in lateral view. Abbreviations: dm = dorsal margin; vm = ventral margin; am = anterior margion; pr = posterior ridge; vr = ventral ridge; om = opercular measurement; no = notch; ha = hyomandibular articulation site; pm = posterior margin; . Scale bars = 2.0 mm.

r^2 values typically greater than 0.95 and mean percent prediction errors generally less than 10% (Table 7).

Diagnostic bones

For each of the bones examined here, clear differences in diagnostic features exist among family taxa. Distinguishing bone characteristics were also evident among genera within the families Gadidae and Clupeidae. Differences between two species from the same genus (*Alosa*) were, however, difficult to discern from the three bones used here. Therefore, bone illustrations are presented for only nine species, with alewife, rather than blueback herring, representing the genus *Alosa*.

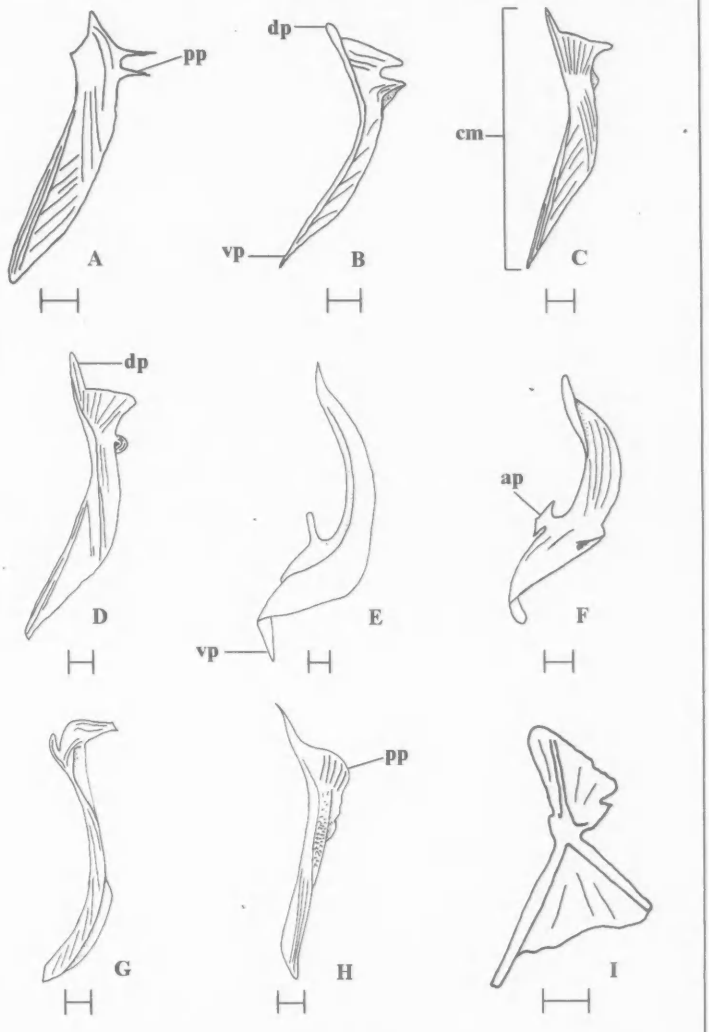

Figure 2

Left cleithra from nine species of marine fishes in the Northwest Atlantic: (**A**) silver hake; (**B**) red hake; (**C**) Atlantic cod; (**D**) haddock; (**E**) alewife; (**F**) Atlantic herring; (**G**) Atlantic mackerel; (**H**) butterfish; (**I**) sand lance. Cleithra are presented in lateral view. Abbreviations: pp = posterior process; dp = dorsal process; vp = ventral process; cm = cleithrum measurement; ap = anterior process; Scale bars = 2.0 mm.

Opercles

The opercle is the largest and most dorsal bone in the opercular series, which consists of the opercle, the subopercle, and the interopercle. Together, these three bones provide the skeletal support for the muscular operculum, or gill cover in fishes. The opercle articulates with the opercular process of the hyomandibula. The articulation site is located in the anterodorsal region of the opercle, and represents a consistent morphological feature for orientation of the bone during examination. The opercles of the fishes examined here can be differentiated by two major diagnostic characteristics. First, the general shape of the opercle is clearly unique to several of the families examined. The opercles of some families share a general triangular shape with three well-defined margins, whereas others are not triangular and possess four definable margins. A second distinctive feature is the presence or absence of ridges originating at the site of hyomandibular articulation and extending ventrally or posteriorly along the margins of the opercle.

Of the taxa examined here, silver hake (*Merluccius bilinearis*) and red hake (*Urophycis chuss*) have opercles with the most pronounced triangular shape and three clearly defined margins (Fig. 1, A and B). The hake opercles are further distinguished by the presence of two prominent ridges originating at the site of hyomandibular articulation and extending ventrally and posteriorly along the anterior and dorsal margins, respectively. Hake opercles differ

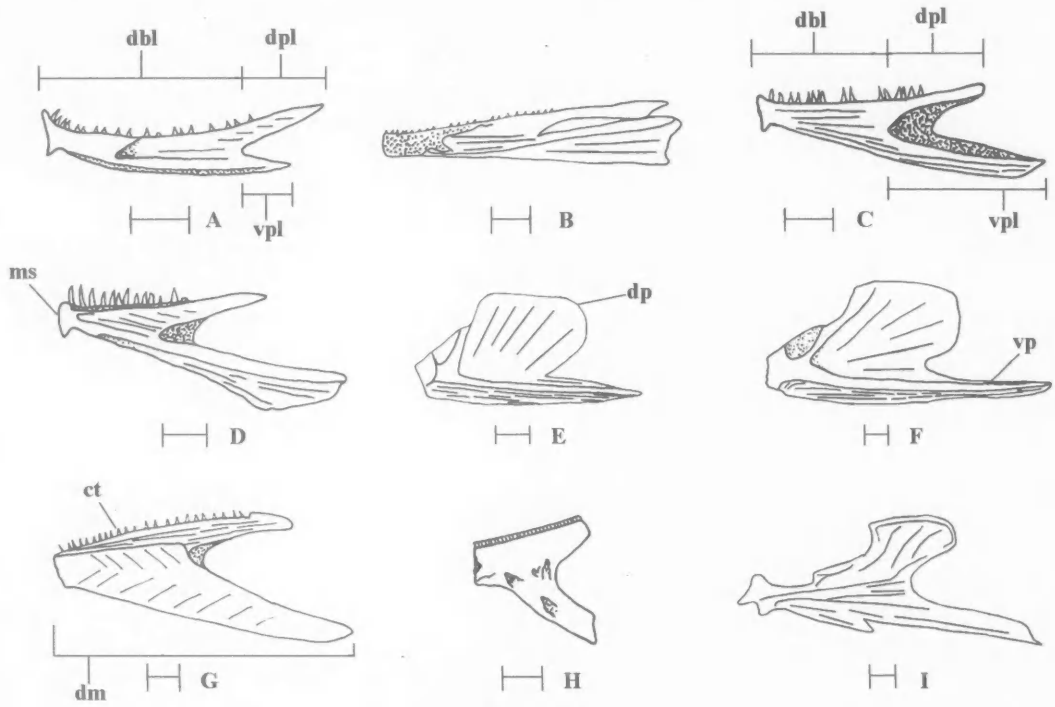

Figure 3

Left dentaries from nine species of marine fishes in the Northwest Atlantic: (**A**) silver hake; (**B**) red hake; (**C**) Atlantic cod; (**D**) haddock; (**E**) alewife; (**F**) Atlantic herring; (**G**) Atlantic mackerel; (**H**) butterfish; (**I**) sand lance. Dentaries are presented in lateral view. Abbreviations: dbl = dentary body length; dpl = dorsal process length; vpl = ventral process length; ms = mandibular symphysis; dp = dorsal process; vp = ventral process; ct = conical teeth; dm = dentary measurement. Scale bars = 2.0 mm.

slightly because the posterior region of the red hake opercle is longer in relation to the body of the opercle than that of silver hake and is also narrower, ending in a sharper point in contrast with the opercle of silver hake. The opercles of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) share a general triangular shape with the hakes, although it is less pronounced in cod and haddock (Fig. 1, C and D). Opercles of Atlantic cod and haddock can be further separated from hake opercles by the presence of only one prominent ridge, which extends posteriorly from the site of hyomandibular attachment, rather than the two ridges found in hake. There appear to be no consistent, observable differences between the opercles of Atlantic cod and haddock. The opercles of alewife (*Alosa pseudoharengus*) and Atlantic herring (*Clupea harengus*) are not triangular and have a distinct notch that is dorsal to the site of hyomandibular articulation along the dorsal margin, with a pronounced curvature along the posterior margin (Fig. 1, E and F). The opercles of alewife and Atlantic herring each possess one ridge, extending ventrally from the site of hyomandibular articulation along the anterior margin, and each also has four definable margins. Alewife and Atlantic herring opercles differ mainly in the shape of the dorsal notch—the notch being cup-shaped in alewife, compared with v-shaped in Atlantic herring. In Atlantic mackerel (*Scomber scombrus*), the opercle has a pronounced dorsal curvature with a notch located centrally along the posterior margin (Fig. 1G). The ridge extending from the hyomandibular articulation site is unique to Atlantic mackerel in that it branches out broadly as it extends posteriorly from the articulation site. The opercles of butterfish (*Peprilus triacanthus*) are unique in general shape, resembling a butterfly wing, with four clearly defined margins and a ridge extending ventrally from the hyomandibular articulation site along the anterior margin (Fig. 1H). Sand lance (*Ammodytes dubius*) represent the only species examined here with opercles not possessing ridges along any margins. Sand lance opercles also

Table 2

Least squares regression equations relating measurements of body depth (BD), eye diameter (ED), caudal peduncle depth (CP), and pectoral–fin length (PF) to total length (TL) and fork length (FL) for ten prey species in the Northwest Atlantic. All measurements are in millimeters. s_b = standard error of the regression coefficient; r^2 = coefficient of determination; %PE = mean percent prediction error; n = number of fish measured; Range = size range in total length. Fork lengths were not measured for red hake, silver hake, or Atlantic cod.

	Total length				Fork length					
Species	Equation	s_b	r^2	%PE	Equation	s_b	r^2	%PE	n	Range
Alewife	$TL = 3.881BD + 11.012$	0.073	0.95	4.38	$FL = 3.469BD + 10.856$	0.067	0.98	4.04	137	73–282
	$TL = 24.906ED - 61.344$	0.781	0.88	7.30	$FL = 23.335ED - 57.728$	0.562	0.96	6.13	137	73–282
	$TL = 12.876CP - 1.784$	0.182	0.97	3.53	$FL = 11.348CP + 1.313$	0.163	0.99	3.31	137	73–282
	$TL = 6.840PF + 0.532$	0.100	0.99	3.15	$FL = 5.982PF + 1.785$	0.093	0.98	3.34	66	73–282
Blueback herring	$TL = 4.970BD + 1.439$	0.268	0.91	3.59	$FL = 4.620BD - 1.573$	0.246	0.91	3.66	38	83–134
	$TL = 25.318ED - 35.605$	2.117	0.80	5.33	$FL = 23.792ED - 37.352$	1.865	0.82	5.42	38	83–134
	$TL = 13.684CP + 0.194$	0.752	0.90	3.53	$FL = 12.585CP - 1.782$	0.754	0.89	4.06	38	83–134
	$TL = 7.760PF + 2.935$	0.383	0.92	3.58	$FL = 7.198PF - 0.005$	0.358	0.92	3.79	38	83–134
Atlantic herring	$TL = 4.561BD + 27.341$	0.089	0.97	4.22	$FL = 4.036BD + 26.880$	0.081	0.97	4.17	84	97–295
	$TL = 26.717ED - 51.235$	0.594	0.96	5.08	$FL = 23.633ED - 42.586$	0.537	0.96	5.00	84	97–295
	$TL = 16.303CP - 17.288$	0.296	0.97	4.55	$FL = 14.441CP - 12.792$	0.257	0.97	4.35	84	97–295
	$TL = 7.507PF + 1.533$	0.101	0.99	2.68	$FL = 6.631PF + 4.306$	0.102	0.98	2.95	84	97–295
Atlantic mackerel	$TL = 5.203BD + 37.203$	0.122	0.97	3.67	$FL = 4.641BD + 39.790$	0.118	0.97	3.89	56	158–330
	$TL = 33.706ED - 81.239$	3.027	0.70	10.83	$FL = 30.404ED - 68.847$	2.652	0.71	10.28	56	158–330
	$TL = 40.081CP - 0.837$	0.700	0.98	2.78	$FL = 35.874CP + 5.213$	0.592	0.99	2.61	56	158–330
	$TL = 9.037PF - 1.242$	0.178	0.98	3.02	$FL = 8.068PF + 5.346$	0.172	0.98	3.06	56	158–330
Butterfish	$TL = 2.860BD + 1.650$	0.038	0.98	3.32	$FL = 2.384BD + 5.638$	0.034	0.98	3.57	108	54–193
	$TL = 20.065ED - 21.148$	0.635	0.90	7.48	$FL = 16.700ED - 13.166$	0.544	0.90	7.52	108	54–193
	$TL = 17.960CP + 7.962$	0.290	0.97	3.57	$FL = 14.950CP + 11.046$	0.264	0.97	4.03	108	54–193
	$TL = 3.766PF + 15.966$	0.060	0.98	4.33	$FL = 3.126PF + 18.121$	0.064	0.98	5.54	63	54–193
Sand lance	$TL = 7.308BD + 58.774$	0.455	0.78	6.07	$FL = 7.045BD + 57.497$	0.463	0.76	6.16	75	109–209
	$TL = 49.467ED - 45.022$	4.358	0.64	8.29	$FL = 47.921ED - 43.479$	4.313	0.63	8.45	75	109–209
	$TL = 35.928CP + 8.185$	1.562	0.88	4.32	$FL = 34.923CP + 7.599$	1.575	0.87	4.48	75	109–209
	$TL = 14.993PF - 31.272$	0.934	0.78	6.52	$FL = 14.542PF - 30.374$	0.933	0.77	6.75	75	109–209
Red hake	$TL = 6.398BD + 10.340$	0.210	0.96	7.40					45	108–340
	$TL = 28.474ED - 91.519$	0.860	0.96	6.37					45	108–340
	$TL = 26.384CP - 17.165$	0.627	0.98	5.18					45	108–340
	$TL = 6.885PF - 0.693$	0.146	0.98	3.92					45	108–340
Silver hake	$TL = 6.460BD + 18.219$	0.164	0.94	7.00					95	75–300
	$TL = 21.998ED - 31.654$	0.504	0.95	7.05					95	75–300
	$TL = 22.823CP + 22.881$	0.345	0.98	4.63					95	75–300
	$TL = 4.946PF + 20.269$	0.070	0.99	3.36					60	75–300
Haddock	$TL = 4.199BD + 21.964$	0.173	0.93	5.30	$FL = 4.066BD + 19.660$	0.164	0.93	4.83	47	79–202
	$TL = 20.069ED - 35.473$	1.375	0.83	7.97	$FL = 19.525ED - 36.724$	1.291	0.84	7.87	47	79–202
	$TL = 18.465CP + 16.596$	0.699	0.94	4.90	$FL = 17.922CP + 14.205$	0.638	0.95	4.54	47	79–202
	$TL = 7.367PF - 10.712$	0.260	0.95	4.69	$FL = 7.106PF - 11.430$	0.263	0.94	4.90	47	79–202
Atlantic cod	$TL = 4.249BD + 21.367$	0.133	0.97	4.03					31	52–140
	$TL = 19.393ED - 19.490$	1.053	0.92	7.33					31	52–140
	$TL = 17.999CP + 9.806$	0.480	0.98	3.72					31	52–140
	$TL = 6.728PF + 7.681$	0.185	0.98	3.48					31	52–140

possess only two clearly definable margins and are curved along the entire posterior margin (Fig. 1I).

Cleithra

In higher teleost fishes, the cleithrum is the ventral most bone of the pectoral girdle, which consists of the supracleithrum, the cleithrum, and the postcleithrum. The cleithrum attaches directly to the scapulocoracoid, which articulates with the base of the pectoral fin. Together, the left and right cleithra form the frame of the body wall directly posterior to the branchial cavity. The cleithra of the fishes examined here can be differentiated by their general shape as

well as the numbers, locations, and shapes of the processes. The majority of the cleithra described here have a gently sloping curvature along the dorsoventral axis, whereas others are clearly more sharply curved. Most families examined here possess cleithra with dorsal and ventral processes that end sharply; others possess varying numbers and shapes of posterior and anterior processes.

The cleithra of silver hake and red hake are gently curved along the dorsoventral axis and each has two posterior processes located directly ventral to the dorsal process (Fig. 2, A and B). The ventral process of the red hake ends in a sharper point and is not as broad as that of silver hake, and the posterior processes are broader than those of silver hake. Atlantic cod and haddock have gently curved cleithra with a general shape similar to that of the cleithra of silver and red hake (Fig. 2, C and D). However, the cleithra of Atlantic cod and haddock contain only one posterior process that is broader than the posterior processes of the hake cleithra, and the dorsal processes of Atlantic cod and haddock cleithra end sharply and are much more pronounced than those of the hake cleithra. The main difference between the cleithra of Atlantic cod and haddock is in the shape of the posterior process; the process is distinctly more hook-shaped in Atlantic cod than in haddock. The cleithra of alewife and Atlantic herring are each sharply curved and possess an anterior process located medially along the dorsoventral axis, which is

Table 3

Least squares regression equations relating measurements of opercle length (OP), cleithrum length (CL), and dentary length (DN) to total length (TL) and fork length (FL) for ten prey species in the Northwest Atlantic. All measurements are in millimeters. s_b = standard error of the regression coefficient; r^2 = coefficient of determination; %PE = mean percent prediction error; n = number of fish measured; Range = size range in total length. Fork lengths were not measured for red hake, silver hake, or Atlantic cod.

	Total length				Fork length					
Species	Equation	s_b	r^2	%PE	Equation	s_b	r^2	%PE	n	Range
Alewife	$TL = 9.851OP - 1.119$	0.126	0.99	2.80	$FL = 8.617OP + 0.307$	0.118	0.99	3.15	66	73–282
	$TL = 7.115CL - 3.450$	0.097	0.99	2.80	$FL = 6.217CL - 1.579$	0.097	0.98	3.22	66	73–282
	$TL = 11.610DN - 23.205$	0.163	0.99	3.23	$FL = 10.144DN - 18.824$	0.163	0.98	3.74	66	73–282
Blueback herring	$TL = 10.014OP + 6.641$	0.547	0.90	3.07	$FL = 9.198OP + 4.259$	0.555	0.88	3.46	38	83–134
	$TL = 7.491CL + 0.161$	0.354	0.93	3.09	$FL = 6.893CL - 1.863$	0.362	0.91	3.40	38	83–134
	$TL = 11.743DN - 11.125$	0.653	0.90	2.96	$FL = 10.871DN - 12.840$	0.621	0.90	3.04	38	83–134
Atlantic herring	$TL = 11.732OP - 0.427$	0.168	0.99	2.30	$FL = 10.405OP + 2.028$	0.168	0.98	2.65	71	97–269
	$TL = 8.752CL - 10.804$	0.126	0.99	2.19	$FL = 7.771CL - 7.353$	0.117	0.98	2.41	71	97–269
	$TL = 10.692DN - 17.263$	0.180	0.98	3.02	$FL = 9.495DN - 13.112$	0.164	0.98	3.10	71	97–269
Atlantic mackerel	$TL = 11.114OP + 0.379$	0.179	0.99	2.01	$FL = 9.867OP + 7.462$	0.163	0.99	2.06	44	158–330
	$TL = 7.789CL - 6.990$	0.067	0.99	1.26	$FL = 6.916CL + 0.889$	0.062	0.99	1.27	44	158–330
	$TL = 12.564DN - 30.649$	0.212	0.99	2.53	$FL = 11.148DN - 19.970$	0.201	0.99	2.44	44	158–330
Butterfish	$TL = 7.956OP + 5.184$	0.299	0.92	7.64	$FL = 6.598OP + 9.279$	0.266	0.91	8.48	63	54–193
	$TL = 5.583CL - 27.802$	0.091	0.98	3.23	$FL = 4.653CL - 18.698$	0.081	0.98	3.43	63	54–193
	$TL = 13.643DN + 6.884$	0.484	0.93	7.49	$FL = 11.309DN + 10.725$	0.436	0.92	8.25	63	54–193
Sand lance	$TL = 18.903OP + 25.655$	1.042	0.82	5.46	$FL = 18.352OP + 24.729$	1.044	0.81	5.60	75	109–209
	$TL = 18.487CL - 1.156$	0.719	0.90	3.81	$FL = 17.938CL - 1.228$	0.741	0.89	4.12	75	109–209
	$TL = 20.785DN - 33.880$	0.772	0.91	3.89	$FL = 20.300DN - 34.146$	0.752	0.91	3.92	75	109–209
Red hake	$TL = 27.956OP - 4.679$	0.612	0.98	4.53					45	108–340
	$TL = 9.061CL - 12.185$	0.123	0.99	2.81					45	108–340
	$TL = 13.870DN - 11.769$	0.291	0.98	4.37					45	108–340
Silver hake	$TL = 17.666OP - 11.964$	0.212	0.99	3.20					60	75–300
	$TL = 7.875CL - 5.271$	0.071	0.99	2.57					60	75–300
	$TL = 8.427DN - 5.149$	0.087	0.99	2.63					60	75–300
Haddock	$TL = 23.040OP - 15.425$	1.053	0.91	5.52	$FL = 22.351OP - 16.804$	0.984	0.92	4.78	47	79–202
	$TL = 6.567CL - 2.688$	0.176	0.97	3.25	$FL = 6.215CL - 1.202$	0.258	0.93	4.87	47	79–202
	$TL = 12.348DN - 3.688$	0.496	0.93	5.07	$FL = 11.680DN - 2.075$	0.606	0.89	6.29	47	79–202
Atlantic cod	$TL = 19.019OP + 7.733$	0.705	0.96	5.43					31	52–140
	$TL = 6.590CL + 1.118$	0.101	0.99	2.50					31	52–140
	$TL = 10.458DN - 5.592$	0.181	0.99	2.29					31	52–140

unique among the fishes examined here (Fig. 2, E and F). The shape of the anterior process differs between the two genera of Clupeidae. In alewife, the anterior process is sickle-shaped, whereas in Atlantic herring, the anterior process is more symmetrical, resembling a mushroom. Additionally, the tip of the ventral process is distinctly sharper in the cleithrum of alewife than in the cleithrum of Atlantic herring. Atlantic mackerel cleithra are gently curved and relatively thin and one posterior process is located in the extreme dorsal region of the bone (Fig. 2G). The dorsal process of the Atlantic mackerel cleithrum is relatively small and rounded, whereas the ventral process is broad and does not end sharply as in the cleithra of the gadids. The cleithra of butterfish are only slightly curved along the dorsoventral axis and contain a broad, rounded posterior process. Butterfish cleithra can be distinguished among the families examined here by the presence of a distinctly sharp, thin dorsal process (Fig. 2H). The cleithra of sand lance have a general

Table 4

Independent variables included in stepwise multiple regression models estimating original fish length. Abbreviations for independent variables are those given in Tables 2 and 3. * indicates that forward and backward models were not identical.

Species	Variables included in forward stepwise model	Variables included in backward stepwise model
Alewife	CP, PF, OP, CL	CP, PF, OP, CL
Blueback herring	PF, CL	PF, CL
Atlantic herring	BD, PF, OP, DN	BD, PF, OP, DN
Atlantic mackerel*	CL, DN	CL
Butterfish*	BD, CP, PF, CL	ED, CP, PF, CL
Sand Lance	CP, DN	CP, DN
Red hake	BD, ED, CL	BD, ED, CL
Silver hake*	OP, CL, DN	CL
Haddock	ED, CP, PF, CL	ED, CP, PF, CL
Atlantic cod	BD, PF, CL, DN	BD, PF, CL, DN

Table 5

Least squares regression equations relating measurements (in millimeters) of body depth (BD), eye diameter (ED), caudal peduncle depth (CP), pectoral fin length (PF), opercle length (OP), cleithrum length (CL), and dentary length (DN) to total weight (W) in grams for ten prey species in the Northwest Atlantic. s_b = standard error of the regression coefficient; r^2 = coefficient of determination; %PE = mean percent prediction error; n = number of fish measured; Range = size range in total length.

Species	Equation	s_b	r^2	%PE	n	Range
Alewife	$W = 0.73 \times 10^{-3} BD^{2.940}$	0.041	0.97	10.74	137	73–282
	$W = 2.62 \times 10^{-3} ED^{4.305}$	0.133	0.89	24.00	137	73–282
	$W = 10.18 \times 10^{-3} CP^{3.194}$	0.037	0.98	8.87	137	73–282
	$W = 1.25 \times 10^{-3} PF^{3.229}$	0.053	0.98	11.31	66	73–282
	$W = 2.95 \times 10^{-3} OP^{3.331}$	0.052	0.98	11.73	66	73–282
	$W = 0.81 \times 10^{-3} CL^{3.383}$	0.051	0.99	10.65	66	73–282
	$W = 1.05 \times 10^{-3} DN^{3.739}$	0.055	0.99	10.66	66	73–282
Blueback herring	$W = 0.64 \times 10^{-3} BD^{3.066}$	0.103	0.96	6.83	38	83–134
	$W = 6.68 \times 10^{-3} ED^{4.049}$	0.340	0.80	15.73	38	83–134
	$W = 13.80 \times 10^{-3} CP^{3.061}$	0.154	0.92	9.48	38	83–134
	$W = 3.94 \times 10^{-3} PF^{2.903}$	0.158	0.90	9.88	38	83–134
	$W = 10.40 \times 10^{-3} OP^{2.851}$	0.160	0.90	9.84	38	83–134
	$W = 2.38 \times 10^{-3} CL^{3.027}$	0.139	0.93	8.15	38	83–134
	$W = 3.00 \times 10^{-3} DN^{3.383}$	0.201	0.89	9.96	38	83–134
Atlantic herring	$W = 2.96 \times 10^{-3} BD^{2.734}$	0.033	0.99	8.64	84	97–295
	$W = 7.14 \times 10^{-3} ED^{4.012}$	0.092	0.96	16.58	84	97–295
	$W = 7.96 \times 10^{-3} CP^{3.438}$	0.060	0.98	11.81	84	97–295
	$W = 3.76 \times 10^{-3} PF^{2.935}$	0.065	0.97	12.06	84	97–295
	$W = 10.53 \times 10^{-3} OP^{3.030}$	0.063	0.97	10.01	71	97–295
	$W = 2.20 \times 10^{-3} CL^{3.193}$	0.069	0.97	10.01	71	97–295
	$W = 3.52 \times 10^{-3} DN^{3.210}$	0.084	0.96	12.87	71	97–295
Atlantic mackerel	$W = 2.79 \times 10^{-3} BD^{2.884}$	0.066	0.97	11.73	56	158–330
	$W = 2.20 \times 10^{-3} ED^{4.762}$	0.377	0.75	39.17	56	158–330
	$W = 247.52 \times 10^{-3} CP^{3.373}$	0.061	0.98	9.12	56	158–330
	$W = 1.49 \times 10^{-3} PF^{3.399}$	0.078	0.97	12.07	56	158–330
	$W = 3.90 \times 10^{-3} OP^{3.318}$	0.049	0.99	6.77	44	158–330

continued

butterfly shape that is clearly unique among the families examined here (Fig. 2I).

Dentaries

The dentary is the largest bone of the lower jaw and bears teeth in many fishes. The posterior region of the dentary is attached directly to the angular and articular bones. The left and right dentaries are fused anteriorly at the mandibular symphysis. The dentaries of the fishes examined here can be differentiated by the presence or absence of teeth and by the relative lengths of the body of the dentary and the dorsal and ventral processes.

The dentaries of silver hake and red hake each possess a row of separate conical teeth extending slightly onto the dorsal process. Teeth are curved inwards and spaced relatively far apart (Fig. 3, A and B). The ratios of the lengths of the dorsal and ventral processes to the length of the body of the

Table 5 (continued)

Species	Equation	s_b	r^2	%PE	n	Range
Atlantic mackerel, continued	$W = 0.76 \times 10^{-3} CL^{3.419}$	0.048	0.99	5.97	44	158–330
	$W = 0.99 \times 10^{-3} DN^{3.760}$	0.093	0.98	10.79	44	158–330
Butterfish	$W = 0.18 \times 10^{-3} BD^{3.138}$	0.026	0.99	7.18	108	54–193
	$W = 7.05 \times 10^{-3} ED^{4.076}$	0.113	0.92	24.59	108	54–193
	$W = 94.11 \times 10^{-3} CP^{2.977}$	0.038	0.98	10.79	108	54–193
	$W = 2.14 \times 10^{-3} PF^{2.795}$	0.039	0.99	10.55	63	54–193
	$W = 3.94 \times 10^{-3} OP^{3.232}$	0.098	0.95	21.39	63	54–193
	$W = 0.06 \times 10^{-3} CL^{3.905}$	0.056	0.99	10.83	63	54–193
	$W = 25.57 \times 10^{-3} DN^{3.197}$	0.085	0.96	19.67	63	54–193
Sand lance	$W = 35.99 \times 10^{-3} BD^{2.245}$	0.063	0.95	10.12	75	109–209
	$W = 11.58 \times 10^{-3} ED^{4.925}$	0.372	0.71	20.83	75	109–209
	$W = 95.52 \times 10^{-3} CP^{3.400}$	0.105	0.94	9.35	75	109–209
	$W = 0.19 \times 10^{-3} PF^{4.366}$	0.274	0.78	20.26	75	109–209
	$W = 34.61 \times 10^{-3} OP^{3.017}$	0.177	0.80	18.38	75	109–209
	$W = 5.07 \times 10^{-3} CL^{3.618}$	0.111	0.94	9.84	75	109–209
	$W = 0.93 \times 10^{-3} DN^{4.258}$	0.242	0.81	17.08	75	109–209
Red hake	$W = 2.82 \times 10^{-3} BD^{2.865}$	0.129	0.92	23.72	45	108–340
	$W = 1.26 \times 10^{-3} ED^{4.492}$	0.153	0.95	19.21	45	108–340
	$W = 44.67 \times 10^{-3} CP^{3.286}$	0.091	0.97	15.93	45	108–340
	$W = 1.23 \times 10^{-3} PF^{3.127}$	0.064	0.98	11.85	45	108–340
	$W = 101.46 \times 10^{-3} OP^{3.073}$	0.077	0.97	13.48	45	108–340
	$W = 1.58 \times 10^{-3} CL^{3.261}$	0.042	0.99	7.34	45	108–340
	$W = 7.61 \times 10^{-3} DN^{3.193}$	0.080	0.97	13.75	45	108–340
Silver hake	$W = 2.39 \times 10^{-3} BD^{2.971}$	0.053	0.97	18.47	95	75–300
	$W = 3.11 \times 10^{-3} ED^{4.081}$	0.114	0.93	30.13	95	75–300
	$W = 211.32 \times 10^{-3} CP^{2.647}$	0.037	0.98	13.88	95	75–300
	$W = 2.47 \times 10^{-3} PF^{2.753}$	0.035	0.99	11.11	95	75–300
	$W = 8.67 \times 10^{-3} OP^{3.458}$	0.044	0.99	11.54	95	75–300
	$W = 0.84 \times 10^{-3} CL^{3.354}$	0.045	0.99	12.40	95	75–300
	$W = 1.10 \times 10^{-3} DN^{3.343}$	0.043	0.99	11.61	95	75–300
Haddock	$W = 2.60 \times 10^{-3} BD^{2.736}$	0.079	0.96	11.69	47	79–202
	$W = 3.32 \times 10^{-3} ED^{4.078}$	0.289	0.82	25.98	47	79–202
	$W = 103.33 \times 10^{-3} CP^{2.865}$	0.100	0.95	15.08	47	79–202
	$W = 0.57 \times 10^{-3} PF^{3.523}$	0.123	0.95	14.97	47	79–202
	$W = 23.77 \times 10^{-3} OP^{3.609}$	0.162	0.92	17.41	47	79–202
	$W = 0.92 \times 10^{-3} CL^{3.296}$	0.085	0.97	11.11	47	79–202
	$W = 7.16 \times 10^{-3} DN^{3.298}$	0.140	0.92	17.77	47	79–202
Atlantic cod	$W = 4.89 \times 10^{-3} BD^{2.558}$	0.062	0.98	12.09	31	52–140
	$W = 5.05 \times 10^{-3} ED^{4.042}$	0.233	0.91	25.68	31	52–140
	$W = 67.74 \times 10^{-3} CP^{2.984}$	0.075	0.98	11.67	31	52–140
	$W = 3.30 \times 10^{-3} PF^{2.987}$	0.078	0.98	12.21	31	52–140
	$W = 73.85 \times 10^{-3} OP^{2.983}$	0.119	0.96	16.51	31	52–140
	$W = 1.15 \times 10^{-3} CL^{3.273}$	0.052	0.99	6.96	31	52–140
	$W = 2.48 \times 10^{-3} DN^{3.498}$	0.071	0.99	9.39	31	52–140

dentary of silver hake are much smaller relative to the same ratios for the red hake dentary. In addition, the teeth of red hake are much less prominent, and the ventral process of the dentary of red hake is considerably broader than that of silver hake. Similar to the dentaries of the hakes, the dentaries of Atlantic cod and haddock also possess a row of separate conical teeth that extend slightly farther onto the dorsal process (Fig. 3, C and D). The length of the dorsal process of the dentaries of Atlantic cod and haddock is much smaller than the length of the ventral process, which contrasts with the dentaries of the hakes. The dentaries of Atlantic cod and haddock can be distiguished by the teeth located just posterior to the mandibular symphysis; the teeth are longer in haddock than in Atlantic cod. Further, the ventral process is considerably broader in haddock than in Atlantic cod. The dentaries of alewife and Atlantic herring each consist of a long, slender ventral process that is considerably longer than the broadly expanded dorsal process, and are toothless (Fig. 3, E and F). The only noticeable difference between the dentaries of the alewife and Atlantic herring is a more gradual incline along the dorsal margin of the dorsal process and a slight hump located anteriorly in Atlantic herring. Similar to the dentaries of the gadids, Atlantic mackerel dentaries possess a row of separate conical teeth (Fig. 3G). However, the teeth of Atlantic mackerel extend well onto the dorsal process, are spaced relatively uniform distances apart, and are not curved inwards. The dentaries of butterfish possess a continuous row of separate teeth that are squared off at the tips, which is a unique feature among the fishes examined here (Fig. 3H). The ventral process of the butterfish dentary extends from the body of the dentary at a considerable angle. In sand lance, the dentaries have a long, thin ventral process that ends sharply and is much longer than the dorsal process, and are toothless (Fig. 3I). The dorsal process of the dentary of sand lance is curved along its margin, similar to the dorsal processes of the dentaries of alewife and Atlantic herring. However, the dorsal process of the dentary of sand lance is much less broad than that found in the dentaries of alewife and Atlantic herring.

Table 6

Independent variables included in stepwise multiple regression models estimating original fish weight. Abbreviations for independent variables are those given in Tables 2 and 3. * indicates that forward and backward models were not identical.

Species	Variables included in forward stepwise model	Variables included in backward stepwise model
Alewife	BD, CP, CL	BD, CP, CL
Blueback herring	BD, CP, PF, CL	BD, CP, PF, CL
Atlantic herring	BD, CP, OP	BD, CP, OP
Atlantic mackerel	OP, CL	OP, CL
Butterfish	BD, CP, PF, CL	BD, CP, PF, CL
Sand Lance	BD, CP, CL, DN	BD, CP, CL, DN
Red hake	CP, PF, CL	CP, PF, CL
Silver hake*	BD, CP, PF, OP	BD, ED, CP, PF, OP, DN
Haddock	BD, CP, CL	BD, CP, CL
Atlantic cod	BD, CP, PF, CL	BD, CP, PF, CL

Table 7

Least squares regression equations relating measurements (in millimeters) of total length (TL) and fork length (FL) to total weight (W) in grams for ten prey species in the Northwest Atlantic. s_b = standard error of the regression coefficient; r^2 = coefficient of determination; %PE = mean percent prediction error; n = number of fish measured; Range = size range in total length. Fork lengths were not measured for red hake, silver hake, or Atlantic cod.

	Total length				Fork length					
Species	Equation	s_b	r^2	%PE	Equation	s_b	r^2	%PE	n	Range
Alewife	$W = 2.74 \times 10^{-6} TL^{3.213}$	0.031	0.99	7.12	$W = 3.29 \times 10^{-6} FL^{3.254}$	0.035	0.99	7.82	137	73–282
Blueback herring	$W = 6.24 \times 10^{-6} TL^{2.993}$	0.101	0.96	6.78	$W = 13.78 \times 10^{-6} FL^{2.887}$	0.113	0.95	7.16	38	83–134
Atlantic herring	$W = 4.10 \times 10^{-6} TL^{3.111}$	0.037	0.99	8.10	$W = 4.53 \times 10^{-6} FL^{3.156}$	0.040	0.99	8.33	84	97–295
Atlantic mackerel	$W = 1.09 \times 10^{-6} TL^{3.354}$	0.039	0.99	5.86	$W = 0.85 \times 10^{-6} FL^{3.451}$	0.041	0.99	5.84	56	158–330
Butterfish	$W = 8.14 \times 10^{-6} TL^{3.094}$	0.024	0.99	6.78	$W = 8.43 \times 10^{-6} FL^{3.180}$	0.032	0.99	8.36	108	54–193
Sand lance	$W = 0.32 \times 10^{-6} TL^{3.449}$	0.112	0.93	12.74	$W = 0.41 \times 10^{-6} FL^{3.421}$	0.119	0.92	13.63	75	109–209
Red hake	$W = 4.41 \times 10^{-6} TL^{3.053}$	0.034	0.99	5.75					45	108–340
Silver hake	$W = 1.91 \times 10^{-6} TL^{3.213}$	0.027	0.99	8.96					95	75–300
Haddock	$W = 3.44 \times 10^{-6} TL^{3.186}$	0.063	0.98	7.50	$W = 3.78 \times 10^{-6} FL^{3.196}$	0.080	0.97	9.12	47	79–202
Atlantic cod	$W = 1.99 \times 10^{-6} TL^{3.308}$	0.090	0.99	5.53					31	52–140

Discussion

Each of the morphometric measurements, including those from diagnostic bones, were significantly related to total length, fork length, and weight. Measurements taken from diagnostic bones, especially cleithrum length, appear to be highly reliable predictors of original size for prey fish species in the Northwest Atlantic. Internal hard parts of fishes have historically proven accurate for estimating original sizes of prey fishes recovered from the stomachs of several freshwater piscivores (Knight et al., 1984; Trippel and Beamish, 1987; Hansel et al., 1988). Our results suggest that examination of diagnostic bones should also benefit diet analyses of marine piscivores.

The ability to estimate original length and weight of common prey fishes from a suite of morphometric measurements should result in a considerable increase in the amount of size-specific diet information for several predatory fishes in the Northwest Atlantic. Accurate information on the sizes of prey consumed across temporal and spatial scales is critical in order to calculate predator consumption rates and to determine predator impact on prey populations. Moreover, many piscivorous fishes feed selectively on specific sizes of prey (Juanes, 1994), suggesting that predatory impact may be greatest on a small range of prey sizes. Therefore, knowledge of prey sizes consumed is necessary in order to determine the extent of size-selective feeding patterns in Northwest Atlantic piscivores and their role in structuring marine fish populations. Finally, several authors have demonstrated the importance of body size in determining the outcome of predator-prey interactions among fishes (Werner and Gilliam, 1984, Miller et al., 1988, Stein et al., 1988). More complete information on predator-prey size relationships in the Northwest Atlantic may improve our understanding of the effects of body size on prey vulnerabilities to predation during various life history stages.

Clearly, the estimation of original prey sizes from diagnostic bone dimensions is not as susceptible to measurement error as estimates from external morphological features, where measurements are usually associated with soft tissues. Moreover, external morphology can often be altered during digestive processes, which may cause some or all external features to yield unreliable measurements. However, for recently consumed prey fishes, external morphological measurements may be highly reliable estimators of original prey size and represent a suitable alternative to diagnostic bones. For example, the linear relations of both eye diameter and caudal peduncle depth with total length were found to be reliable for reconstructing original prey lengths of six prey species consumed by juvenile bluefish (Scharf et al., 1997). Similarly, Serafy et al. (1996) found the linear relation between eye diameter and total length of red drum to be particularly useful in estimating the size of angled fish. In addition to cleithrum length, maximum body depth and caudal peduncle depth were consistent predictor variables for estimating original weight of prey fishes examined in this paper. Differences in fish condition factor may not be closely correlated with differences in other morphological measurements. Therefore, indices of fish girth, such as body depth and caudal peduncle depth, should be reliable indicators of condition factor and should be most closely related to body weight. Further, the reconstruction of original prey sizes from external morphological measurements has the advantage of being comparatively less labor intensive than dissection and removal of internal hard parts.

The reconstruction of original prey sizes from diagnostic bones or external morphological measurements does, however, have some important limitations. The potential effects of preservatives on bone dimensions need to be considered if stomach contents are stored in a chemical preservative. The fish used in this study were not exposed to preservatives but were frozen and thawed before measured. The use of boiling water to aid in the removal of soft tissue may cause shrinkage and deformation of extracted bones if sufficient time elapses between the boiling process and the completion of bone measurements. However, bone measurements for our analyses were completed immediately after dissection and removal. In addition to the potential effects of preservation, previous studies indicate that estimation of prey sizes from partial remains will likely underestimate the proportion of small prey fish in the diet, because bones and external features of larger prey fish should be more resistant to digestion and be recovered from piscivore stomachs more frequently (Trippel and Beamish, 1987; Hansel et al., 1988). Lastly, allometric relationships may not remain constant with changes in fish size. Therefore, regression equations should not be applied to fish outside the size range used for their generation.

The results of our study indicate that, for the families of fishes examined, the opercle, cleithrum, and dentary represent diagnostic tools that can potentially aid in the identification of prey fishes recovered from the stomachs of Northwest Atlantic piscivores. The diagnostic features unique to each of the three bones appear to perform equally well in distinguishing family taxa from one another. However, within the families Gadidae and Clupeidae, cleithra and dentaries are better suited to illustrate

differences between genera relative to opercles. Newsome (1977) and Hansel et al. (1988) revealed similar findings, demonstrating the limitations of opercles for identifying prey fishes beyond the family level. Moreover, Hansel et al. (1988) found that cleithra and dentaries were more resistant to digestion than opercles or pharyngeal arches, when examining several freshwater fishes, and concluded that, for young prey fish, the cleithrum may be the most reliable bone because of its large size and early development in relation to other diagnostic bones.

None of the three diagnostic bones appear useful for differentiating between the two species of the genus *Alosa* examined in this study. Similarly, Hansel et al. (1988) found that for certain congeneric freshwater fishes, identification was inconsistent and not dependable when opercles, cleithra, dentaries, and pharyngeal arches were used. The size range of fishes used in this study included juveniles and young adults (Table 1) and is typical of size ranges examined in previous studies (Trippel and Beamish, 1987; Hansel et al., 1988). Therefore, for these life stages, opercles, cleithra, and dentaries may be potentially useful as tools for identifying prey fishes to the family and, in some cases, the generic taxonomic level, but likely are not adequate for distinguishing between species of the same genus.

Our descriptions of the diagnostic bones provide a simple means to distinguish prey fishes based on general bone structure. Indeed, there have been more rigorous efforts directed at identifying the systematic relationships among several of the fishes examined in this paper. However, the bone descriptions in this paper were provided as a simple guide for field identification of prey fishes commonly recovered from piscivore stomachs, and thus centered on general overall shape and features that were common to all of the fishes. The differences among the taxa that are outlined here should be readily observable to a large range of workers with varying levels of fisheries training. Therefore, we suggest that the level of analysis and description presented here may compliment existing information and may be ideally suited for identification of prey fishes in field settings.

The bone descriptions and regressions presented in this paper clearly have the potential to increase the amount of dietary information obtainable from stomach contents analyses of Northwest Atlantic piscivores. Further, the generation of a series of regression equations relating measurements from both internal hard parts and external morphological features to original fish size may provide a means to cross reference prey size estimates, thus facilitating the identification of erroneous estimates.

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Marine turtle populations on the west-central coast of Florida: results of tagging studies at the Cedar Keys, Florida, 1986–1995

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Abstract.—Large-mesh tangle nets were used to collect marine turtles in Waccasassa Bay, near the Cedar Keys, Florida, from June 1986 to October 1995. Tagging records were analyzed to determine the species composition, population structure, and seasonal occurrence of Kemp's ridley, *Lepidochelys kempii*, loggerhead, *Caretta caretta*, and green, *Chelonia mydas*, turtles. Additional information on local movements, morphometrics, growth, population estimation, and diet was provided for Kemp's ridley turtles. Subadult green turtles dominated the catch on the seagrass shoals of Waccasassa Reefs. Subadult Kemp's ridley turtles and, to a lesser degree, subadult and adult loggerhead turtles were primarily captured near the oyster bars of Corrigan Reef. Marine turtles were caught in these nearshore waters from April to November. Recaptures indicate that some Kemp's ridley turtles remain in the vicinity of Corrigan Reef during their seasonal occurrence and return to this foraging area annually. Seasonal and annual size distributions of Kemp's ridley turtles were investigated and regression equations were developed for carapace morphometrics. Carapace growth averaged 4–5 cm/yr for Kemp's ridley turtles, but growth analyses were confounded by the extrapolation of annual estimates from short-term recaptures. Population estimates for the Kemp's ridley mark-recapture data indicated a mean annual population size of 159 turtles at Corrigan Reef with presumably high rates of immigration and emigration by larger subadult turtles. Examination of fecal samples indicated that crabs were the primary food items of Kemp's ridley turtles captured near oyster bars.

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Historical information concerning marine turtles in the coastal waters of Florida is limited to landing statistics and observational data associated with the commercial turtle fishery (Ehrhart, 1983). During the late 1800s, large-mesh tangle nets were used to catch significant numbers of green turtles, *Chelonia mydas*, in the Indian River Lagoon and around the Cedar Keys (True, 1887; Brice, 1896). These turtles were exported to markets in the northeastern United States. Kemp's ridley, *Lepidochelys kempii*, and loggerhead turtles, *Caretta caretta*, were also captured and used as a food resource in local markets, but the landings of these species were not recorded in fisheries reports (Witzell, 1994a). The Florida fishery for marine turtles was greatly reduced by 1900 (Ingle and Smith, 1949). However, there are no quantitative data to demonstrate accurately that depletion had occurred as a result of overfishing (Caldwell and Carr, 1957). The lack of definitive data is further complicated by the fact that most of the fishery statistics reported for Florida after 1900 include green turtles imported from Costa Rica and Nicaragua by way of Key West, and no distinction was made between turtles caught in Florida and those imported from the Caribbean (Ingle and Smith, 1949; Caldwell and Carr, 1957; Witzell, 1994a, 1994b).

The first scientific investigations and conservation efforts for marine turtles were implemented fifty years after the reduction of the turtle fishery. Ingle and Smith (1949) and Carr (1952) outlined scientific data necessary for the protection and restoration of green turtles throughout their range. Carr and Caldwell (1956) conducted a one-year tagging study of green and Kemp's ridley turtles purchased from Cedar Key fish houses and provided the first details on size ranges, morphometrics, local movements, growth rates, and population estimates for these species. Florida enacted legislation in 1956 that prohibited the take of nesting female turtles and their eggs (Caldwell and Carr, 1957; Ehrhart, 1983).

Restrictions were imposed on the Florida turtle fishery in 1971, which consisted of closed seasons and size limits (Ingle, 1972). By 1978, all species of marine turtles were listed as threatened or endangered in the Endangered Species Act and protected under federal legislation.

Listing marine turtles in the Endangered Species Act outlawed their harvest and prompted surveys on nesting beaches and adjacent coastal waters in Florida (Carr et al., 1982). Entanglement nets, designed similarly to those formerly used in the turtle fishery, were employed to capture green and loggerhead turtles inhabiting the northern Indian River Lagoon System (Ehrhart and Yoder, 1978; Mendonça, 1981, 1983; Mendonça and Ehrhart, 1982; Ehrhart, 1983). These fishery-independent studies provided the first biological data on population size and structure, growth rates, and activity patterns for the previously exploited species of marine turtle in the lagoonal habitat. Trawls associated with the commercial shrimp fishery were used to collect turtles occurring in and around the Port Canaveral ship channel (Carr et al., 1980; Henwood, 1987; Henwood and Ogren, 1987). Information obtained from these fishery-dependent surveys includes size class distribution, seasonal occurrence, and migrations of loggerhead, Kemp's ridley, and green turtles.

In 1984, the National Marine Fisheries Service (NMFS) initiated long-term tagging studies of marine turtles occurring in the coastal waters of Florida, with emphasis placed on the critically endangered Kemp's ridley turtle (Ogren, 1989; Schmid and Ogren, 1990, 1992). Rudloe et al. (1991) reported on the size-class distribution, seasonal occurrence, and variations in carapace length by season and water depth for Kemp's ridley turtles incidentally captured in commercial fisheries of northwest Florida. Tagging records of turtles captured in the east-central Florida shrimp fishery provided additional data on species composition, size-class distribution, seasonal occurrence and migrations, morphometric relationships, and growth data for marine turtles along the Atlantic coast (Schmid, 1995). Fishery-independent capture techniques have also been used to collect marine turtles in the nearshore waters of west-central Florida and preliminary results of these efforts have been given by Schmid and Ogren (1990, 1992). The present paper analyzes tagging records collected near the Cedar Keys, Florida, from 1986 to 1995 in order to determine the species composition, population structure, and seasonal occurrence of Kemp's ridley, loggerhead, and green turtles. Additional information on local movements, morphometrics, growth, population estimation, and diet are provided for Kemp's ridley turtles.

Materials and methods

Study area

Marine turtles were collected east of the Cedar Keys in Waccasassa Bay, which is located on the west coast of Florida (Fig. 1). The northern and eastern boundaries of Waccasassa Bay are saltmarsh coastline inundated by numerous tidal creeks. The Waccasassa River flows into the northeast corner of the bay and is the main contributor of freshwater to the estuarine system (Wolfe, 1990). The western edge of the bay is semi-enclosed by the Cedar Keys, whereas the southern portion is open to tidal exchange with the Gulf of Mexico. Corrigan Reef, located in northwestern Waccasassa Bay, and Waccasassa Reefs, located in the eastern half of the bay, are the prominent geographic features of this shallow embayment.

Netting efforts were concentrated at three sites along Corrigan Reef (Fig. 1; site 1: 29°09'N, 82°58'W; site 2: 29°08'N, 82°58'W; and site 3: 29°07'N, 82°58'W), approximately 5 km east of the Cedar Keys. Corrigan Reef comprises a series of oyster (*Crassostera virginica*) beds in the northern region (site 1) and oyster shell bars in the southern region (sites 2 and 3). Limestone outcroppings occur among the mud and sand flats and in channels on the periphery of oyster bars. Netting was also conducted at the outer shoal of Waccasassa Reefs (29°06'N, 82°53'W), approximately 12 km east-southeast of the Cedar Keys. Waccasassa Reefs are composed of three seagrass shoals with a broad, deep-channel cutting midway through each shoal. The tides in both of these areas are mixed, with two highs and two lows of variable amplitude. Strong tidal currents flow through the channels, particularly during the new and full moon phases (spring tides).

Data collection

Seasonal netting was conducted at Corrigan Reef from 1986 to 1991 and at Waccasassa Reefs from 1986 to 1988 (see Table 1 for effort and months fished each year). A full year of sampling was performed at Corrigan Reef in 1992 and 1993. Water temperatures were recorded sporadically from 1986 to 1991 and monthly for 1992 and 1993. Netting surveys were performed for 1–3 days every other week during the neap tides. One or two nylon mesh tangle nets (61- or 51-cm stretch mesh, 20 meshes deep, and 65 m length) were set across a channel at a given site and fished over a 6- to 12-hour tidal cycle. Nets were checked hourly or immediately after an entangled turtle had been sighted. Research efforts shifted from netting surveys to telemetric monitoring during 1994

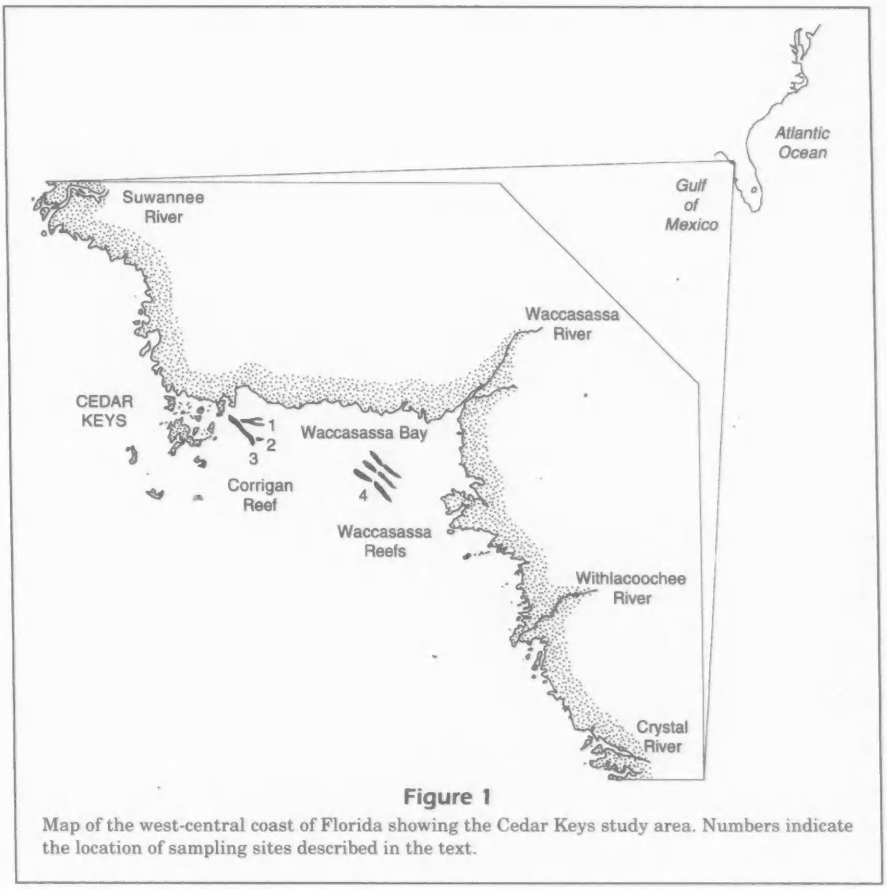

Figure 1

Map of the west-central coast of Florida showing the Cedar Keys study area. Numbers indicate the location of sampling sites described in the text.

Table 1

Annual effort (km-h) and CPUE (turtles/km-h) by species for Corrigan Reef and Waccasassa Reefs from 1986 to 1993. Lk=*Lepidochelys kempii*, Cc=*Caretta caretta*, and Cm=*Chelonia mydas*.

Year (months)	Corrigan Reef				Waccasassa Reefs			
	Effort	Lk/h	Cc/h	Cm/h	Effort	Lk/h	Cc/h	Cm/h
1986 (Jun–Nov)	153.9850	0.1104	0.0065	0.0000	9.3275	0.0000	0.0000	0.1072
1987 (May–Dec)	236.0963	0.0720	0.0000	0.0042	19.6300	0.0000	0.0509	0.2547
1988 (May–Sep)	142.3988	0.2388	0.0070	0.0000	1.2675	0.7890	0.0000	0.0000
1989 (Jun–Sep)	177.4500	0.1634	0.0394	0.0113	—	—	—	—
1990 (Jun–Sep)	233.4150	0.1499	0.0129	0.0000	—	—	—	—
1991 (Jun–Oct)	152.5225	0.1246	0.0000	0.0000	—	—	—	—
1992 (May–Dec)	461.5650	0.1148	0.0303	0.0022	—	—	—	—
1993 (Jan–Oct)	124.8000	0.1923	0.0160	0.0000	—	—	—	—

and 1995, and tag data collected on these turtles were included in the analyses.

The following morphometric measurements (Pritchard et al., 1983) were recorded for each turtle: total straight-line carapace length (TSCL, anterior most edge of carapace to posterior margin of postcentral); standard straight-line carapace length (SSCL, nuchal notch to posterior margin of postcen-

tral); minimum straight-line carapace length (MSCL, nuchal notch to notch between postcentrals); minimum curved carapace length (MCCL, nuchal notch to notch between postcentrals); and straight-line carapace width (CW) at the widest point. Straight-line carapace lengths and width were measured to the nearest 0.1 inch with forester's calipers. Curved carapace length was measured to the nearest 0.1 cm with a flexible fiberglass measuring tape. Weight (WT) was measured to the nearest 0.25 lb with a spring scale. All measurements were performed by the author to avoid individual differences in measuring technique (Bjorndal and Bolten, 1988) and were converted to metric units for analysis. Notes on the condition of the turtle were recorded when the animal was injured or deformed (e.g. tag scars, carapace wounds, etc.).

Turtles were double tagged on the trailing edge of the fore flippers with no. 681 Inconel tags (June 1986 to May 1988; May 1994 to October 1995), with Jumbo Roto plastic tags (June 1988 to October 1991), or with both (May 1992 to September 1993). Beginning in 1988, two holes were drilled in specific marginal scutes of Kemp's ridley turtles in order to identify the year of capture (1988—left postcentral, 1989—right postcentral, 1990—left 12th marginal, 1991—right 12th marginal, 1992—left 11th marginal, 1993—right 11th marginal, 1994—left 10th marginal, and 1995—right 10th marginal). Passive integrated transponder (PIT) tags were applied to the left front flipper of Kemp's ridley turtles from June 1992 to October 1995. Turtles were immediately released after data collection approximately 100 m down-current from the netting site.

Data analysis

Marine turtle life history stages were defined according developmental habitats and carapace lengths (Schmid, 1995). The term "juvenile" was reserved for immature turtles in the epipelagic stage of development. A turtle was considered "subadult" after recruiting to its respective coastal-benthic habitat and "adult" when sexually mature. Loggerhead turtles greater than 80 cm (Carr, 1986), green turtles greater than 83 cm (Witherington and Ehrhart, 1989), and Kemp's ridley turtles greater than 60 cm (Pritchard and Márquez M., 1973) were considered adult based on sizes of nesting females.

Capture records were analyzed to evaluate species composition within the Cedar Keys study area, length-frequency distribution of each species, and patterns of seasonal occurrence. Additional analyses of morphometrics, growth rates, population estimates, and dietary composition were performed for Kemp's ridley turtles. Standard straight-line carapace length was used in the analyses of size distribution and growth. Means are followed by ± one standard deviation unless noted otherwise. Turtle catch per unit of effort (CPUE) was standardized according to Shaver (1994) with the formula

$$E = \left(\frac{Nets \times Length}{1000} \right) Hrs,$$

where E = the netting effort in hours fished by a 1-km tangle net;
$Nets$ = the number of tangle nets fished;
$Length$ = the length (m) of a net; and
Hrs = the number of hours fished.

Kemp's ridley turtle morphometric relationships were investigated by regressing carapace width on length and log-transformed weight on length. Conversion formulae for Kemp's ridley turtle carapace lengths were calculated by regressing paired straight-line and curved carapace lengths. Turtles with carapace wounds or deformities were not included in regression equations.

Yearly growth rates for Kemp's ridley turtles were calculated with the formula

$$G = \left(\frac{\Delta Length}{Days} \right) 365,$$

where G = the growth rate in cm/yr;
$\Delta Length$ = difference between the recapture length and the initial length; and
$Days$ = the number of days at large.

Growth rates were grouped and analyzed in terms of the recapture interval duration, recaptures between versus recaptures within netting seasons, and size classes of recaptured turtles. Growth rates were assigned to 10-cm size classes on the basis of mean of the initial and recapture carapace measurements (Bjorndal and Bolten, 1988). The von Bertalanffy growth interval equation was fitted to the recapture data with a nonlinear least-squares regression procedure (SAS Institute Inc., 1989). The von Bertalanffy growth interval equation (Fabens, 1965) for recapture data is:

$$CL_2 = a - (a - CL_1)e^{-kt},$$

where CL_2 = the carapace length at recapture;
a = the asymptotic length;
CL_1 = the length at first capture;

k = the intrinsic growth rate; and
t = the time in years between captures.

Kemp's ridley turtle mark-recapture data for 1986–93 were tallied in a method B table (Krebs, 1989) and analyzed with the computer program JOLLY (Hines, 1988; Pollock et al., 1990). Summary statistics for the Jolly-Seber computer analysis include the total number of turtles captured and released each year (n), the number of marked (m) and unmarked (u) turtles captured each year, the number of turtles released each year that are captured again later (r), and the number of turtles captured before a given year and captured again later (z). The data were applied to a Jolly-Seber model that assumes that the population parameters survival rate (Φ) and capture probability (p) are constant per unit time. Annual estimates of the number of marked turtles in the population (M), population size (N), and the number of individuals recruited to the population (B) were computed with the reduced parameter model.

Dietary analyses were conducted on Kemp's ridley fecal specimens fortuitously encountered during the tagging process. Fecal specimens were initially examined in the field and the contents were noted in tagging records. Additional examinations were performed from photographs and samples of feces. Components of the feces were identified to the lowest taxon possible and were analyzed to determine the percentage of specimens containing each component (Burke et al., 1994). Nomenclature of molluscs was identified by using the field guide of Abbott and Morris (1995).

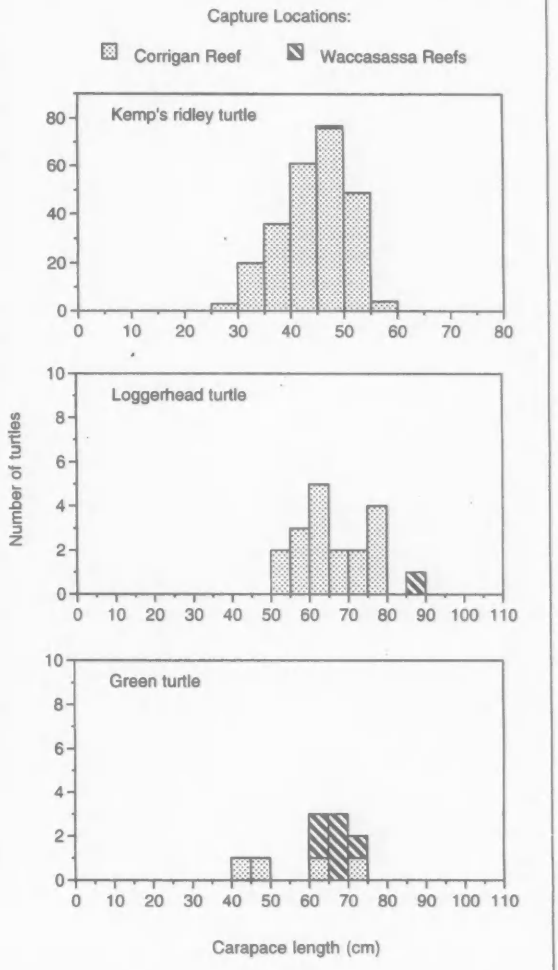

Figure 2

Length-frequency distributions for Kemp's ridley turtles, *Lepidochelys kempii*, loggerhead turtles, *Caretta caretta*, and green turtles, *Chelonia mydas*, collected in Waccasassa Bay, Florida, from 1986 to 1995. Note the different scale in y axis of upper graph.

Results

Marine turtle captures and effort

One (12.5%) Kemp's ridley, 1 (12.5%) loggerhead, and 6 (75%) green turtles were collected during 64.75 h of netting at Waccasassa Reefs. The Kemp's ridley turtle measured 47.6 cm SSCL, the loggerhead turtle measured 86.4 cm SSCL, and green turtles ranged from 63.0 to 73.9 cm SSCL (mean=68.0 ±3.9 cm; Fig. 2). Three of the green turtles captured at Waccasassa Reefs exhibited fibropapillomas (1–4 cm diameter), primarily in the axillary region of the flippers. Maximum CPUE for green turtles at Waccasassa Reefs was 0.255 turtles/km-h in 1987, and values of CPUE for loggerhead and Kemp's ridley turtles were 0.051 turtles/km-h in 1987 and 0.789 turtles/km-h in 1988, respectively (Table 1). Netting effort was conducted at this location from June through November and turtles were captured in July and August.

Two hundred and fifty-three (91.7%) Kemp's ridley, 19 (6.9%) loggerhead, and 4 (1.4%) green turtles were collected during 980.00 h of netting at Corrigan Reef. Kemp's ridley turtles ranged from 26.8 to 58.6 cm SSCL (mean=44.5 ±6.3 cm), loggerhead turtles ranged from 50.0 to 77.4 cm SSCL (mean=65.0 ±8.7 cm), and green turtles ranged from 42.9 to 70.9 cm SSCL (mean=56.8 ±12.9 cm; Fig. 2). Loggerhead turtles greater than 80 cm SSCL were caught at

Corrigan Reef but could not be landed for data collection. One such turtle was identified as a male because its tail extended considerably beyond the posterior marginal scutes. Fibropapillomas were not observed on green turtles captured at Corrigan Reef. Annual CPUE for Kemp's ridley turtles at Corrigan Reef ranged from 0.072 turtles/km-h in 1987 to 0.239 turtles/km-h in 1988 (Table 1). Maximum CPUE for loggerhead and green turtles at Corrigan Reef was 0.039 turtles/km-h and 0.011 turtles/km-h in 1989, respectively. Kemp's ridley and loggerhead turtles were captured in this area from April to November, whereas green turtles were captured from June to September.

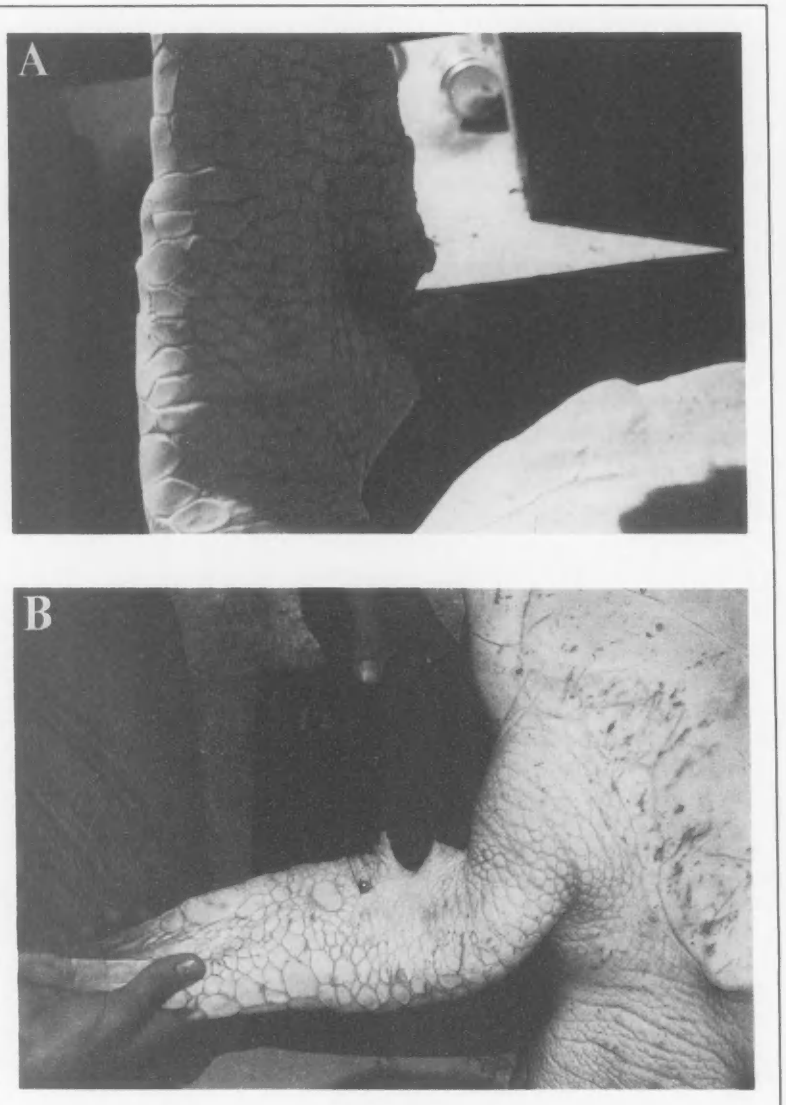

Figure 3

Photographs of recaptured Kemp's ridley turtles, *Lepidochelys kempii*, demonstrating (**A**) a barnacle-encrusted tag and (**B**) a flipper scar from tag loss.

Recaptures and local movements

Thirty-four Kemp's ridley turtles (23 with tags and 11 with tag scars), five loggerhead turtles (3 with tags and 2 with tag scars), and one green turtle (with a tag scar) were identified as recaptures. All recaptured turtles with tags, with the exception of two NMFS Galveston laboratory headstart Kemp's ridleys, were initially captured and tagged at Corrigan Reef. Thirty-five percent of the recaptured turtles exhibited tag scars, which is indicative of moderate tag loss and may account for the lack of recaptures or recoveries in other areas. Schmid and Ogren (1992) identified barnacle fouling as a potential problem with the otherwise corrosion-resistant Inconel flipper tag. The increased drag and weight produced by the barnacle clusters and the necrosis of flipper tissue by the encrusted tag (Fig. 3A) resulted in the eventual shedding of the tags and the formation of a conspicuous notch in the trailing edge of the flippers (Fig. 3B). Barnacle growth was observed on both Inconel and plastic tags in as little as 14 days and tag loss was observed within 10 months after application. Similar retention times were noted for both types of tags, but a quantitative analysis of retention rates was not performed because of small sample sizes. The use of marginal markings allowed for the identification of tag-scarred turtles originally tagged at the Cedar Keys and the tabulation of recapture data by year classes. PIT tags were successfully used to identify tag-scarred Kemp's ridley turtles in the later part of the study.

Kemp's ridley recaptures ranged from 14 to 839 days and loggerhead recaptures ranged from 142 to 189 days. The two headstart Kemp's ridley turtles were recaptured approximately 3–4 years after their release in Texas waters as was determined from the location of the living tag in the carapace (Fontaine et al., 1993; Caillouet et al., 1995). Seven Kemp's ridley turtles with tag scars had marginal scute markings indicating the year of initial capture at Corrigan Reef. Four of these were at large for 1 year, one was at large for 2 years, and two were at large for 3 years. Four Kemp's ridley turtles had multiple recaptures in the vicinity of Corrigan Reef. One turtle was tagged at site 2 in September 1991 and recaptured at this site in October 1991 and May 1992 (0.7 year duration). Another turtle tagged at site 1 in July 1990 was recaptured at this site in June 1991 and June 1992 (1.9-year duration). A turtle tagged at site 2 in October 1991 was recaptured at this site in September 1992 and at site 3 in May 1994 (2.6-year duration). The fourth turtle had a 1991 marginal marking and was recaptured at site 2 in September 1993 and August 1995 (≈4-year duration).

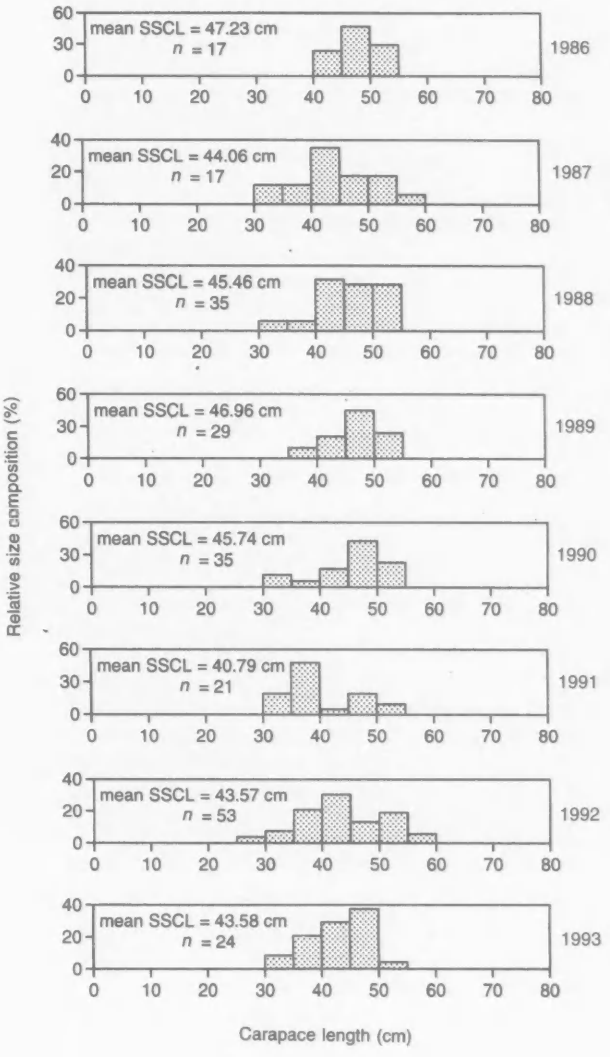

Figure 4

Annual relative size composition of Kemp's ridley turtles, *Lepidochelys kempii*, captured at Corrigan Reef from 1986 to 1993.

Seasonal and annual size distributions

Mean water temperatures at Corrigan Reef were calculated by season (Table 2): winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov). Turtles were captured in water temperatures greater than 20°C. Carapace lengths for Kemp's ridley turtles captured from 1986 to 1995 were pooled by season (spring, summer, or fall) according to the month of capture (Table 2). A significant difference (F=3.76, P=0.025) was detected between the mean SSCL of at least two seasons. Multiple comparisons with the Bonferroni procedure demonstrated no significant difference in mean SSCL between spring and summer, or spring and fall. However, mean SSCL in summer was significantly larger than that of fall.

Analysis of the annual relative composition of Kemp's ridley turtle carapace lengths from 1986 to 1993 indicated that the 40–50 cm size class dominated the catch during all years except 1991 (Fig. 4). The majority of turtles captured during 1991 were in the 30–40 cm size class. The carapace length distributions for 1986 through 1990 were not significantly different when compared with the Kolmogrov-Smirnov two-sample test. The distribution of carapace lengths for 1991 was significantly different from all years except 1987, and the distribution for 1992 was significantly different from all years except 1987 and 1988. The carapace length distribution for 1993

Table 2

Seasonal water temperatures and Kemp's ridley turtle, *Lepidochelys kempii*, carapace lengths at Corrigan Reef from 1986 to 1995 (standard deviations given in parentheses).

Season	Mean water temperature	Mean carapace length	*n*	Size range
Spring	22.5°C (3.0)	44.1 cm (7.4)	24	26.8–58.6 cm
Summer	30.4°C (0.6)	45.5 cm (5.9)	142	28.2–54.4 cm
Fall	22.9°C (4.2)	43.1 cm (6.6)	85	27.3–56.6 cm
Winter	15.7°C (2.0)	—	0	—

was not significantly different from the distributions of 1986 through 1990. The observed shift in size-class distribution for 1991 may have been caused by changes in fishing conditions that year. Beginning in July 1991, a smaller mesh (25.4-cm bar) net was deployed either singly or in combination with the larger mesh (30.5-cm bar) net that was used the previous years. The smaller mesh net may have resulted in the increased capture of 30–40 cm turtles in 1991, although the frequency of 40–50 cm turtles increased in the following years. Also, during August 1991, a massive influx of pelagic Sargassum occurred along the west coast of Florida and the majority of netting effort was conducted in the months following this unusual event. It is not known how this latter condition may have affected the relative frequency of carapace lengths, either by increasing the frequency of 30–40 cm turtles or decreasing the frequency of 40–50 cm turtles.

Carapace regression equations

There was a strong correlation between carapace width and carapace length (r=0.9883, n=227) for Kemp's ridley turtles. Regression of width on length resulted in the equation

$$CW = -3.7415 + 1.0530\ (SSCL).$$

A strong correlation (r=0.9886, n=225) was calculated for the weight-to-length data transformed with the natural logarithm. Regression of these variables resulted in the equation

$$\ln WT = -8.1570 + 2.8128\ (\ln SSCL).$$

Conversion equations were computed between the straight-line and curved carapace length measurements (Table 3). These equations will allow for comparisons between studies with different measuring techniques.

Table 3

Formulae for converting between straight-line and curved carapace measurements of Kemp's ridley turtles, *Lepidochelys kempii*. TSCL = total straight-line carapace length, SSCL = standard straight-line carapace length, MSCL = minimum straight-line carapace length, and MCCL = minimum curved carapace length.

Converted length	Conversion formula	*n*	r^2
TSCL	1.0118 SSCL + 0.0650	227	0.9990
TSCL	1.0214 MSCL + 0.3800	227	0.9982
TSCL	0.9720 MCCL + 0.2203	107	0.9920
SSCL	0.9874 TSCL – 0.0199	227	0.9990
SSCL	1.0094 MSCL + 0.3155	227	0.9990
SSCL	0.9598 MCCL + 0.1941	107	0.9929
MSCL	0.9773 TSCL – 0.2896	227	0.9982
MSCL	0.9897 SSCL – 0.2658	227	0.9990
MSCL	0.9495 MCCL – 0.0864	107	0.9933
MCCL	1.0205 TSCL + 0.1368	107	0.9920
MCCL	1.0345 SSCL + 0.1162	107	0.9929
MCCL	1.0462 MSCL + 0.3913	107	0.9933

Growth analyses

Twenty-one Kemp's ridley turtles were recaptured a total of 24 times, yielding 24 annual growth rates. However, 83% of the recaptures occurred within a year of initial tagging and extrapolating annual growth rates from short-term recapture intervals will amplify any error associated with the measurements. The removal of short-term recaptures decreased the range of annual growth rates and increased the precision of the mean growth rate estimate (Table 4A). Subsequent analyses of growth by netting seasons and size classes were confounded by short-term recaptures. The mean growth rate of Kemp's ridley turtles recaptured within netting seasons (see Table 1 for months fished each year) was significantly larger (χ^2=7.93, df=1, P=0.005) than that of turtles recaptured between netting seasons (Table 4B). However, the duration of all recaptures within netting seasons was less than 180 days (mean=49.6 ± 44.5 days) and the annual growth rates may have been overestimated owing to extrapolation error. Although mean growth rates did not vary significantly when compared by size class (F=0.753, P=0.484), Kemp's ridley turtles in the 40–50 cm size class appeared to have a higher mean growth rate than those in the 30–40 cm and the 50–60 cm size classes (Table 4C).

Deletion of data with recapture intervals less than 90 days reduced the mean growth rate of the 40–50 cm size class (4.7±3.0 cm/yr; n=9, range: 2.9–12.3 cm/yr).

The von Bertalanffy growth interval equation was fitted to each of the recapture interval data treatments. Estimates of asymptotic length ranged from 77.3 to 91.4 cm and estimates of intrinsic growth rate ranged from 0.0852 to 0.1167 (Table 5). The growth interval equation for all Kemp's ridley turtles recaptured at Cedar Key had the lowest residual mean square, a standard that has been used to select the best fit growth model (Dunham, 1978). However, the estimated asymptotic length for this model (a=91.4 cm) is considerably larger than the average carapace length reported for nesting females (65 cm; Márquez M., 1994) and should therefore be considered biologically unrealistic (Frazer et al., 1990). The estimated asymptotic length for recapture intervals greater than 180 days (a=77.3 cm) would be more appropriate if this latter criterion is used. This model has the least amount of error from short-term recaptures, but suffers from a reduced sample size and a truncated range of carapace lengths.

Population estimations

The computer program JOLLY computed a survival rate of 0.41 (± 0.07 SE) and a capture probability of 0.18 (±0.05 SE) for Kemp's ridley turtles at Corrigan Reef. Population estimates ranged from 98.05 turtles in 1987 to 262.79 turtles in 1992 (Table 6). For 1987 through 1993, the mean annual population size was 158.50 (±112.40 SE) turtles and there was a mean of 15.35 (±11.58 SE) marked turtles in the population (10% of the estimated mean population size). For 1987 through 1992, there was a mean annual recruitment of 102.71 (±48.23 SE) turtles (65% of the estimated mean population size).

Food

Fecal specimens from 12 Kemp's ridley turtles were examined during the course of this study. Crab components were identified in all specimens. In addition, two (17%) of the fecal specimens contained mollusc shells and two (17%) specimens contained a portion of undigested seagrass (*Halodule wrightii* in one and *Halophila engelmannii* in the other). Seven (58%) of the fecal specimens contained unidentified crab fragments. Five (42%) of the turtles had consumed chelipeds of stone crab, *Menippe* spp., and three (25%) had consumed chelipeds of blue crab, *Callinectes sapidus*. Two (17%) Kemp's ridley turtles had consumed shark eye shells (*Polinices duplicata*), one of which also consumed a common eastern nassa shell (*Nassarius vibex*), that contained hermit crabs (Paguridae). The two turtles that consumed hermit crabs also ingested mollusc components. Cancellate cantharus shells (*Cantharus cancellarius*) and oys-

Table 4

Mean annual growth rates of Kemp's ridley turtles, *Lepidochelys kempii*, by recapture interval, netting season, and size class (standard deviations given in parentheses). Turtles were assigned to size classes by mean of initial and recapture SSCL.

Data treatments	n	Mean SSCL growth rate (cm/yr)	Range of growth rates (cm/yr)
Recapture interval			
All recaptures	24	5.4 (3.3)	1.2–13.0
Recaptures > 90 days	16	4.5 (2.6)	1.2–12.3
Recaptures > 180 days	13	3.6 (1.2)	1.2–5.4
Netting season			
Within season	10	7.7 (3.6)	1.7–13.0
Between seasons	11	3.3 (1.1)	1.2–4.7
Size class			
30–40 cm	7	4.6 (2.8)	1.2–9.4
40–50 cm	13	6.2 (3.7)	2.9–13.0
50–60 cm	4	4.6 (2.5)	2.2–7.9

Table 5

Estimated values of asymptotic length (a) and intrinsic growth rate (k) from nonlinear regression of von Bertalanffy growth interval equation for Kemp's ridley turtles, *Lepidochelys kempii* (one asymptotic standard error in parentheses).

Data treatment	n	a	k
All recaptures	24	91.4 cm (41.9)	0.0852 (0.0720)
Residual mean square error = 1.3872			
All recaptures > 90 days	16	90.9 cm (51.1)	0.0858 (0.0892)
Residual mean square error = 2.1179			
All recaptures > 180 days	13	77.3 cm (29.2)	0.1167 (0.0957)
Residual mean square error = 2.0085			

Table 6

Summary statistics and estimated parameters for the Jolly-Seber analysis of Kemp's ridley turtle, *Lepidochelys kempii*, mark-recapture data (standard errors given in parentheses). Descriptions of the notation are as follows: n = total number of turtles captured and released each year; m = number of marked turtles captured each year; u = number of unmarked turtles captured each year; r = number of turtles released each year that were captured again later; z = number of turtles captured before a given year and captured again later; M = annual estimate of the number of marked turtles in the population; N = annual estimate of population size; and B = annual estimate of the number of individuals recruited to the population.

	Summary statistics					Estimated parameters		
Year	n	u	m	r	z	M	N	B
1986	17	17	0	3	—	—	—	—
1987	17	16	1	3	2	10.91 (5.49)	98.05 (32.11)	139.87 (42.90)
1988	35	31	4	1	1	18.20 (7.41)	187.03 (55.83)	96.38 (32.86)
1989	29	28	1	3	1	7.30 (4.70)	159.79 (50.22)	107.25 (34.87)
1990	32	29	3	2	1	14.17 (6.72)	172.66 (52.53)	45.54 (24.72)
1991	20	18	2	6	1	11.32 (6.05)	109.35 (35.92)	201.60 (58.21)
1992	49	43	6	2	1	28.61 (10.55)	262.79 (75.59)	25.64 (28.35)
1993	22	19	3	—	—	16.34 (9.53)	119.81 (39.34)	—

ter shell fragments were identified in both of the fecal specimens. Furthermore, one of these specimens contained hooked mussels (*Ischadium recurvus*) attached to an oyster shell fragment.

Discussion

The results of this study indicate the importance of seagrass beds and oyster reefs as developmental habitats for Kemp's ridley, loggerhead, and green turtles. Furthermore, these species may be preferentially utilizing the two habitat types on the basis of their respective feeding strategies. The extensive seagrass flats along the west coast of Florida have been identified as foraging habitat for the herbivorous green turtle (True, 1887; Carr and Caldwell, 1956; Caldwell and Carr, 1957). Netting effort at the seagrass shoals of Waccasassa Reefs resulted in captures of mid- to late subadult green turtles, comparable to the size class of green turtles reported by Carr and Caldwell (1956). The Kemp's ridley turtle is primarily cancivorous (Shaver, 1991; Burke et al., 1994), and the distribution of this species can be correlated to areas with abundant crab populations (Ogren, 1989). Intertidal oyster bars provide refuge for stone crabs (McRae, 1950; Bender, 1971; Wilber and Herrnkind, 1986), whereas the mud bottom adjacent to these bars is the preferred substrate of blue crabs (Evink, 1976; Wolfe, 1990). Subadult Kemp's ridley turtles dominated the aggregation of marine turtles captured in the vicinity of Corrigan Reef and the food items for these turtles were typical of the macroinvertebrate fauna inhabiting nearshore oyster bars. Subadult and adult loggerhead turtles were also captured at Corrigan Reef; this species also feeds on benthic invertebrates, particularly molluscs (Dodd, 1988). The possibility of competition for food resources between loggerhead and Kemp's ridley turtles is unknown and could be investigated by comparing fecal specimens of both turtles captured in the same location.

Tagging studies of Kemp's ridley turtles have revealed reproductive migrations of females in the Gulf of Mexico (Pritchard and Márquez M., 1973), seasonal migrations of subadults along the Atlantic coast (Henwood and Ogren, 1987; Schmid, 1995), and an east–west movement of subadults in the northern Gulf (Ogren, 1989). However, there are no mark-recapture data to indicate a seasonal migration of subadult turtles in the eastern Gulf of Mexico. As stated by Carr (1980) and observed in the present study, turtles apparently immigrate to the nearshore waters of the Cedar Keys in April and emigrate to some

unknown locality in November, presumably in response to changes in water temperature. Ogren (1989) suggested a seasonal offshore movement of Kemp's ridley turtles in the northern Gulf on the basis of capture of subadult turtles in deeper waters off Apalachicola Bay during the winter (Rudloe et al., 1991). Satellite telemetry has demonstrated that Kemp's ridley turtles on the Atlantic coast respond to a decrease in water temperature by moving to warmer waters southward or offshore (Renaud, 1995). Marine turtles in the Cedar Keys area could be moving westward to deeper waters offshore or southward within the shallow coastal waters. Alternatively, some Cedar Key fishermen believe that turtles overwinter in the remote coastal waters by "burying up" in mud bottom holes (Carr and Caldwell, 1956; Schmid and Ogren, 1990). Loggerhead turtles have exhibited this behavior in the Port Canaveral ship channel at water temperatures below 15°C (Carr et al., 1980; Ogren and McVea, 1982). Water temperatures as low as 12–14°C were recorded at the Cedar Keys study area from December to February. The possibility of winter dormancy or migration (or both) by west coast turtles requires additional information (Ogren and McVea, 1982) and could be investigated by attaching satellite transmitters to turtles during the fall.

Recaptures of Kemp's ridley turtles tagged and released in the northeastern Gulf of Mexico have provided information on their use of coastal foraging grounds. Carr and Caldwell (1956) observed that Kemp's ridley and green turtles released from Cedar Key returned to the Withlacoochee-Crystal River fishing grounds within a short period of time. The authors implied that the turtles may be exhibiting a homing behavior and maintaining home ranges at the site of initial capture. Schmid and Ogren (1990) suggested that Kemp's ridley turtles in the Florida panhandle region were transitory because of the lack of long-term recaptures (Rudloe et al., 1991). By comparison, recaptures in the Cedar Keys area were indicative of a more residential aggregation. Although the majority of Kemp's ridley turtles tagged near the Cedar Keys were recaptured within a year of initial capture, almost equal numbers of turtles were recaptured within netting seasons and between netting seasons. Recaptures within a netting season suggest that some turtles remain in the vicinity of Corrigan Reef during their seasonal occurrence in this region. Recaptures between netting seasons indicate that some turtles return to the previously utilized oyster bar habitat annually and may do so for up to four years. Efforts are currently underway to determine the activity patterns and habitat associations of Kemp's ridley turtles in the Cedar Keys area (Schmid, 1994).

Kemp's ridley turtles were numerous in the coastal waters of Florida prior to the 1950s (Carr, 1980). Data provided by Carr and Caldwell (1956; p. 21, Fig. 3) indicated that approximately 1% of the Kemp's ridley turtles captured at the Withlacoochee-Crystal River fishing grounds were early to mid-subadults (20–40 cm), 88% were mid- to late subadults (40–60 cm), and 11% were adult (60+ cm). There was also an unconfirmed report of a vitellogenic female weighing 42 kg with an estimated length of 75 cm. The presence of adult turtles in this 1955 survey corresponds to a period when there were relatively large, though declining, nesting aggregations of Kemp's ridley turtles (U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). The lack of 20–40 cm turtles may be indicative of lower subadult recruitment resulting from the intensive egg harvesting that was occurring at this time (Hildebrand, 1982). In contrast, the catch at the Cedar Keys from 1986 to 1995 comprised 24% early to mid-subadults and 76% mid- to late subadults. Observations and captures of adult Kemp's ridley turtles at sea have become extremely rare owing to the greatly reduced nesting population, whereas the higher frequency of 20–40 cm turtles may suggest higher subadult recruitment as a result of nesting beach protection (Ogren, 1989).

Carr and Caldwell (1956) also described an apparent, though not statistically significant, seasonal shift in the mean carapace length of Kemp's ridley turtles taken in the commercial turtle fishery. Larger turtles (mean=54.9 cm) were captured early in the April to November fishing season, whereas smaller turtles predominated the mid- and late season catch (mean=50.3 cm and 52.1 cm, respectively). The seasonal mean carapace lengths reported in this earlier study were 5–10 cm greater than those recently recorded at the Cedar Keys. The authors' description of their measurement technique (". . . from the center of the anterior end of the carapace and the greatest posterior projection of the carapace.") corresponds to the standard straight-line carapace length. Furthermore, the entanglement nets used in the present study were the same mesh size as those used in the commercial turtle fishery. The perceived difference could be due to preference by the former turtle fishermen for larger, higher-priced turtles. Alternatively, the smaller mean carapace lengths of the present study may be indicative of an increased aggregate of smaller Kemp's ridley turtles along the west coast of Florida.

Despite numerous tagging studies, there is very little information available on the growth rates of wild Kemp's ridley turtles (Márquez M., 1994). The data treatments used to analyze Kemp's ridley turtle

growth at the Cedar Keys indicated an average increase of 4–5 cm/yr in carapace length. Growth rates of 6–9 cm/yr were obtained for Kemp's ridley turtles at Cape Canaveral with the same data treatments (Schmid, 1995). The higher growth rates observed for east coast turtles are possibly due to measurement errors identified in the Cape Canaveral study. Error was minimized in the Cedar Key study because all measurements were determined by the author using the same equipment and techniques. Assuming a constant growth rate of 4–5 cm/yr, a Kemp's ridley turtle would require 8–10 years to grow from a 20-cm postpelagic subadult (Ogren, 1989) to a 60-cm adult. An estimate of 10–12 years to maturity is calculated by combining the duration of the subadult stage with the estimated 2-year pelagic juvenile stage (Schmid and Ogren, 1990). This calculated age to sexual maturity is in agreement with Kemp's ridley growth models computed from skeletochronological age estimates (Zug and Kalb, 1989; Zug, 1990) and the combination of recapture data for Cape Canaveral and Cedar Keys (Schmid and Witzell, 1997).

The Kemp's ridley turtle aggregation at the Cedar Keys was considered an open "population" with recruitment in terms of postpelagic turtles and subadult immigrants from other locations and with losses in terms of death and permanent emigration to other subadult or adult aggregations. Annual estimates from the Jolly-Seber analysis were indicative of the catchable turtle population at Corrigan Reef within the months fished, which may or may not be representative of the entire aggregation in this area (Krebs, 1989). The relatively low number of recaptures, and corresponding low estimated capture probability, reduced the precision of the population estimates as evidenced by their high standard errors (Pollock et al., 1990). Nonetheless, general comments can be made concerning the estimates of recruitment and survival of Kemp's ridley turtles in the Cedar Keys area. The majority of turtles captured in this locality were mid- to late subadults; there were very few captures of postpelagic turtles. Therefore, provided that sampling bias due to the large-mesh nets was minimal, the high level of recruitment estimated from the Jolly-Seber analysis was presumably a result of immigration by larger subadult turtles. The low estimated survival rate was probably a function of emigration rather than high turtle mortality. However, there were no recaptures of turtles tagged at Cedar Key to indicate emigration to other localities and there was no systematic sampling of turtle strandings to demonstrate the extent of mortality in this region.

In conclusion, tagging studies conducted at the Cedar Keys are models for characterizing foraging populations of marine turtles and these efforts must be expanded to include regions not yet sampled in order to accurately manage these threatened and endangered species (Magnuson et al., 1990; Thompson et al., 1990; U.S. Fish and Wildlife Service and National Marine Fisheries Service, 1992). Areas where marine turtle congregate need to be identified through anecdotal information, historical records, incidental captures, and stranding data. In-water sampling programs should be conducted over an extended period of time to establish the distribution and abundance of turtles in areas of aggregation. After implementing a mark-recapture study, supplementary research activities may include the following: holding turtles for fecal sample collection; sampling blood for stress response, sex determination, and genetic analyses; monitoring local movements via radio and sonic telemetry; discerning migrations via satellite telemetry; and developing GIS models for marine turtle habitat associations.

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Effects of hypoxia and temperature on survival, growth, and respiration of juvenile Atlantic sturgeon, *Acipenser oxyrinchus**

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Abstract.—Hypoxia in Chesapeake Bay has increased during the past century, coincident with the disappearance of Atlantic sturgeon spawning stocks. We hypothesized that Atlantic sturgeon young-of-the-year (YOY) might be more susceptible than other estuarine fishes to high temperature and low oxygen conditions, now prevalent in Chesapeake Bay. Atlantic sturgeon (10–70 g) were reared under conditions of hypoxia (2–3 mg/L dissolved oxygen) and normoxia (6–7 mg/L) at 19°C and 26°C for 10 days. High-temperature hypoxia resulted in lower survival (mean=6.3%) and respiration rate (mean=0.136 mg O_2/(g·h)). Low-temperature hypoxia resulted in a mean survival of 78% and mean respiration rate of 0.212 mg/(g·h). Under hypoxia, mean weight-specific growth rate was 1.27%/d, ca. threefold less than growth under normoxia. Temperature alone did not significantly affect growth rates. When sturgeon were denied access to the surface, growth rates were significantly diminished in both normoxic and hypoxic treatments. At low ambient oxygen levels and high temperature, denial of surface access was fully lethal within 30 hours. We conclude that increased incidence of summertime hypoxia during this century has degraded sturgeon nursery habitats in Chesapeake Bay.

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An economically important population of Atlantic sturgeon, *Acipenser oxyrinchus*, once inhabited Chesapeake Bay. During the late nineteenth century, Chesapeake Bay supported the second greatest caviar fishery in the eastern United States (Murawski and Pacheco, 1977). In the early 1900s, the population collapsed. In Maryland, fishery landings declined from 74,500 kg, in 1904, to 320 kg in 1920 (Hildebrand and Schroeder, 1928). Atlantic sturgeon have not recovered in Chesapeake Bay (Spier and O'Connell, 1996). The last fish legally harvested in Chesapeake Bay, a mature female, was captured in 1970 from the Potomac River. The spawning population of Atlantic sturgeon may have been extirpated from Chesapeake Bay (Speir and O'Connell, 1996; Grogan and Boreman[1]).

State, federal, academic, and nonprofit organizations have begun to mobilize public interest and support for an aquaculture-based restoration program for Atlantic sturgeon in Chesapeake Bay. A principal assumption for Atlantic sturgeon restoration is that deleterious conditions that led to the extirpation of the population (e.g. loss of habitat or over fishing) are now abated. Therefore, it is critical to evaluate possible causes for Atlantic sturgeon extirpation from Chesapeake Bay before state and federal agencies move forward with a large-scale aquaculture-based restoration program.

We hypothesize that increased hypoxia in Chesapeake Bay resulted in reduced habitat for Atlantic sturgeon and contributed to their decline. During this century, periodic increases (albeit small) in Atlantic sturgeon abundances have occurred in the southern and northern extent of the species' range (Murawski and Pacheco, 1977). However, no evidence exists for periodic recoveries of Atlantic sturgeon in Chesapeake Bay. The period of population decline and low abundance in Chesapeake Bay corresponds to a period of poor water quality, from 1950 to present, caused by increased nutrient loading and increased spatial and temporal frequency of hypoxia (Officer et al., 1984; Mackiernan, 1987; Jordan et al., 1992; Kemp et al., 1992; Cooper and Brush, 1993).

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The goal of the study was to investigate the effects of dissolved oxygen and temperature on growth, survival, and respiration of juvenile (young-of-the-year) Atlantic sturgeon. High temperatures are known to amplify negative effects of hypoxia on growth and survival of estuarine fishes (Coutant, 1985). Habitats in Chesapeake Bay that satisfy both temperature and dissolved oxygen (DO) preferences of Atlantic sturgeon may be limiting during the summer as have been demonstrated for striped bass (Coutant and Benson, 1990; Brandt and Kirsch, 1993). In this study we define hypoxia as oxygen concentrations <4.0 mg/L. Hypoxia has been defined previously as <2 mg/L for Chesapeake Bay (Phil et al., 1991; Harding et al., 1992), an ambient oxygen level that is detrimental to benthic infaunal production. This definition, however, may be too stringent for fishes because oxygen concentrations at this level are often lethal (Brett, 1970; Jordan et al., 1992).

A nested-multifactorial experiment was designed to investigate the effects of temperature and dissolved oxygen on growth, respiration, and survival of young-of-the-year Atlantic sturgeon. During the course of our experiments we observed that fish in hypoxic conditions frequently surfaced, often breaking the surface of the water with their snout. Therefore we included surface access as a third factor in our investigation—whether this behavior might benefit growth and survival under conditions of oxygen stress.

Methods

Experimental material

Juvenile Atlantic sturgeon were obtained from the U.S. Fish and Wildlife Service, Northeast Fishery Center, Lamar, Pennsylvania (Hendrix, 1995). During June 1995, Center personnel collected a large female (2.4-m total length) and three male Atlantic sturgeon from the Hudson River near Hyde Park (River km 135). Fish were transported to the Center for artificial spawning and for larval rearing. Larvae and early juveniles were reared at the Center at 17°C and 1 ppt salinity. A failure in the water heating system at the Center caused juveniles, age 45 to 60 days after hatching, to experience low water temperatures, ca. 10°C. At 60 days after hatching, 500 juveniles (0.3–2.0 g wet weight) were transported in an oxygenated container to Chesapeake Biological Laboratory and acclimated to 19°C and 2 ppt salinity over a 10-d period. Juveniles were reared in sixteen 40-liter tanks and fed Biokyowa© fry feed (700–2000 µm diameter) ad libitum until they were ca. 5 grams wet weight (>10 cm total length) and large enough to be handled with little or no stress for scute-clips (see below).

Nested growth and survival experiments

A nested multivariate experiment (Fig. 1) evaluated survival and growth rates in relation to access to surficial water (sealed or unsealed tank), temperature (~20°C and ~26°C), dissolved oxygen (~3 mg/L or ~7 mg/L), and tank replication. The nested design directed the analysis of variance to occur in hierarchical order at four levels. The model of the nested design for growth rate was

$$y_{ijklm} = \mu + \tau_i + \beta_{j(i)} + \gamma_{k(ij)} + \theta_{\lambda(ijk)} + \varepsilon_{(ijkl)m},$$

where y_{ijklm} = the growth rate response by individual juveniles;
μ = overall mean;
τ_i = the effect of the ith surface access category;
$\beta_{j(i)}$ = the effect of the jth temperature;
$\gamma_{k(ij)}$ = the effect of the kth oxygen level;
$\theta_{l(ijk)}$ = the effect of the lth tank (replicate); and
$\varepsilon_{(ijkl)m}$ = the random error component.

The model of the nested design for survival rate was

$$S_{ijkl} = \mu + \tau_i + \beta_{j(i)} + \gamma_{k(ij)} + \varepsilon_{l(ijk)},$$

where S_{ijkl} = the arcsine-transformed survival rate for each replicate.

Statistical significance for factors was accepted at $\alpha = 0.05$ (type-I sum of squares for type-I error). To remove possible effects due to differences in fish size among experiments and experimental levels, initial fish weight was included in ANOVAs as a covariate. Calculations of variances and significance tests were performed by using PC-SAS, PROC NESTED (SAS, 1982). Survival data were arcsine transformed to meet assumptions of normally distributed error.

Four 10-day experiments were conducted under the four combinations of surface access, temperature, and dissolved oxygen, each replicated twice. In the high-temperature hypoxia treatments, high mortality was observed. Because we wished to have greater confidence in associating low survival with high-temperature hypoxia, we repeated the treatments with surface access and high temperature (at both low and high DO levels) for a total of four replicates (Fig. 1).

Experimental tank dimensions were 78-cm diameter, 46-cm height, and 220-liter volume. External

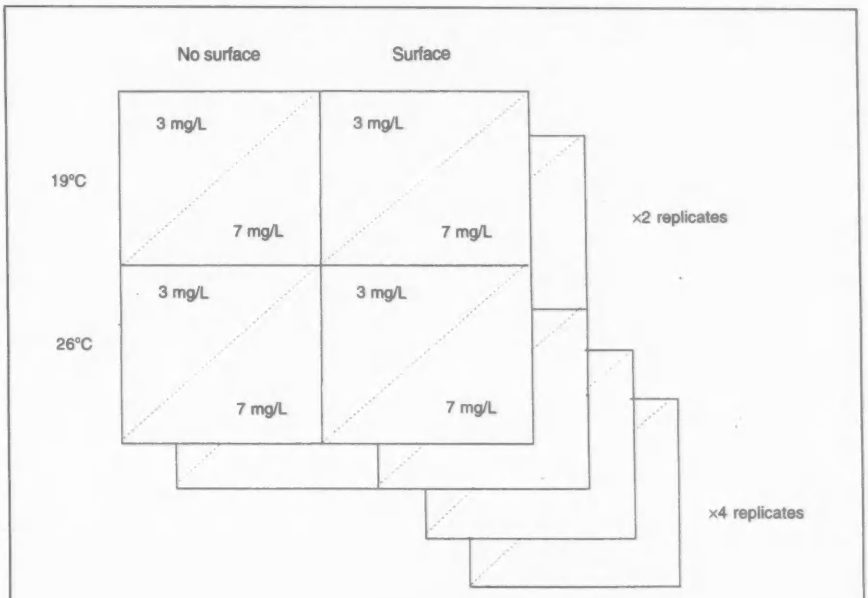

Figure 1

Nested experimental design. Replicates are presented as layers. Dissolved oxygen rates (3 or 7 mg/L) were nested within temperature and surface access levels.

stand-pipes for flow-through water allowed sturgeon to use the entire bottom surface. During the experiments clear plexiglass lids were attached to the tanks with clamps and duct tape. A large hole (5-cm diameter) in each lid, fitted with a stopper, permitted access to the tank for feeding of fish, for periodic checks of water quality, and for removal of dead individuals. Hoses for air and water supply also passed through the lid. In the tanks that permitted access to the air-water interface, water level was maintained at 5 cm below the lid. In treatments designed to limit access to the surface, lids were sealed to the tank and tanks were filled completely. Two head tanks delivered water at either 19°C or 26°C to experimental tanks, each maintained at a rate of 1.2 –1.5 L of flow-through water/min. Dissolved oxygen was controlled by maintaining hypoxic conditions in head-tanks and by adding aeration directly to normoxic treatment tanks. Hypoxic levels (2.5–3.0 mg/L) were maintained in head-tanks by mixing hypoxic well water (<2 mg/L) with oxygenated Patuxent estuary water (6 mg/L). Thus, salinity varied slightly between experiments but was always within the range 1.5–3 ppt. When necessary, water was aerated to bring oxygen levels to 2.5 mg/L in the head-tank. Normoxic treatment water was a mixture of well water and Patuxent estuary water. Dissolved oxygen levels were well mixed (homogenous) in the tanks owing to their shallow design, flow-through water, and constant swimming of YOY sturgeon. Lighting was provided on a 12:12 h light:dark cycle.

With the exception of the 26°C and no-surface-access treatment, temperature and oxygen concentrations were maintained within 10% of their prescribed levels (19 or 26°C, 3 or 7 mg/L). In the 26°C sealed experiment, aeration supplied to the head-tank was insufficient to attain oxygen conditions close to 7 mg/L for the normoxic treatment (mean replicate dissolved oxygen concentrations were 5.10 and 5.25 mg/L). In the hypoxic sealed treatment (mean replicate dissolved oxygen concentrations were 3.76 and 4.44 mg/L), dissolved oxygen was deliberately held above 3 mg/L because this level with high temperature had been observed previously to be lethal in unsealed tanks. Despite these elevated "hypoxic" conditions, the combination of high temperature and low oxygen was fully lethal in the sealed tanks (see below).

Juveniles (8 to 30 grams wet weight) were acclimated to experimental conditions over a 4-d period. On day 0 of each experiment, lengths and wet weights (juveniles weighed in water on a top-loading balance) were recorded and a dorsal scute(s) clipped to identify each individual. In preliminary trials, we found that scute clips did not significantly affect growth

rate. Regeneration of the scute did not obscure the clip during the 10-d experiments. Six to eight juveniles were placed in each experimental tank and fed the formulated diet (2-mm pellets) at 2.5% body weight per day. Fish were fed at 06:00, 10:00, 14:00, 18:00, and 20:00 h. Water quality was checked during feeding times and any remaining food or feces were siphoned prior to feeding. Food amounts were adjusted when mortalities occurred. On day 10 of the experiment, individual weights and lengths were recorded. Weight-specific absolute and instantaneous growth rates were determined for the experimental period according to Ricker (1975). In instances where juveniles died before the end of the experiment, individuals surviving >3 days of experimental conditions were included in the analysis of treatment effects on growth.

Respiration experiment

Respiration was estimated over a 42-h period for four combinations of temperature (19 or 26°C) and dissolved oxygen (~3 or ~7 mg/L) each replicated once. Juveniles were acclimated for a 4-day period and starved 12 h prior to the start of respiration measures. Seven juveniles were weighed (in water) and placed in each tank "respirometer." The tanks were sealed (no air gap). Oxygen levels were maintained by aerating the head-tanks, rather than each experimental tank. There was no feeding during the 42-h experiments. Inflow and outflow temperature, salinity, oxygen content, and flow rate were measured in experimental and control "blank" tanks (Cech, 1990) at 06:00, 10:00, 14:00, 18:00 and 22:00.

Experimental conditions of temperature were maintained within 1°C of the prescribed treatment level (19 or 26°C) (Table 1). Oxygen levels varied substantially from the prescribed levels between temperatures. For the hypoxic treatments, oxygen was provided at significantly higher levels (P=0.001) at 26°C (4.09 ±0.07 mg/L) than at 19°C (2.51 ±0.05 mg/L). This was intentional because survival and growth experiments had shown that DO levels <3.5 mg/L in concert with high temperature were lethal. Despite this precaution, all fish at 26°C and at low oxygen level perished within 24 hours. At the high-level DO treatments, oxygen conditions were ca. 1 mg/L higher at 19°C than at 26°C. Total biomass of the 7 fish per tank ranged from 157.6 to 248.2 grams (Table 1).

Respiration (i.e. oxygen uptake) was estimated (Cech, 1990) as

$$R = (M_E - M_C)/B$$
$$M_{E,C} = \left((C_I - C_O\right)V$$

where R = weight-specific O_2 consumption rate (mg O_2/(g·h);
$M_{E,C}$ = O_2 consumption rate in experimental E or control C tanks (mg O_2/h);
B = combined wet weight (biomass) of sturgeon juveniles (g);
C_I = O_2 concentration in inflowing water (mg O_2/L);
C_O = O_2 concentration in outflowing water (mg O_2/L); and
V = water flow rate (L/h).

Results

Survival

Deaths were observed only in hypoxic treatments (Table 2). At hypoxic level, survival was substantially lower at 26°C (mean=6.3% survival) than at 19°C

Table 1

Replicate tank environmental conditions and respiration rates (mean ± standard error) for respiration experiment. Dissolved oxygen (DO) levels, low or high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. Inflow oxygen and tank temperature refer to actual conditions provided to tanks. Biomass is the total initial weight of the seven sturgeon used in each replicate.

Temperature level	DO level	Inflow oxygen mg/L	Tank temperature	Biomass (g)	Respiration rate mg O_2/g·h
26°C	Low	3.762 ± 0.163	25.20 ± 0.04	216.6	0.175 ± 0.042
		4.436 ± 0.209	25.34 ± 0.02	181.3	0.103 ± 0.030
	High	6.310 ± 0.075	25.54 ± 0.02	188.1	0.245 ± 0.028
		6.259 ± 0.088	25.47 ± 0.02	179.6	0.307 ± 0.020
19°C	Low	2.536 ± 0.029	19.51 ± 0.02	196.3	0.202 ± 0.028
		2.495 ± 0.020	19.43 ± 0.02	157.6	0.214 ± 0.022
	High	7.361 ± 0.060	19.73 ± 0.06	189.5	0.228 ± 0.028
		7.273 ± 0.058	19.67 ± 0.04	249.2	0.207 ± 0.020

Table 2

Replicate tank deaths during the nested survival and growth experiment. Experiments are labeled according to the temperature treatment and whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Dissolved oxygen (DO) levels, low and high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. Rep. = replicate(s).

Experiment	DO level	Rep.	Experimental day										Survival (%)
			1	2	3	4	5	6	7	8	9	10	
26°C unsealed 1	Low	1			6	1	1						0
		2			2		4					2	0
		3		4			1	2	1				0
		4				1		1		1	1		50
26°C unsealed 2	High	1											100
		2											100
		3											100
		4											100
26°C sealed	Low	1	8										0
		2	7	1									0
	High	1											100
		2											100
19°C unsealed	Low	1			1		1						75
		2			1			1					75
	High	1											100
		2											100
19°C sealed	Low	1							1				88
		2						1	1				75
	High	1											100
		2											100

(mean=78.3% survival). No significant difference was found in overall survival rate between sealed and unsealed tanks (P=0.54). In unsealed tanks, deaths were distributed throughout the 10-d experimental period. In the 26°C sealed-hypoxic level tanks, all individuals succumbed within the first 30 hours of the experiment. Moribund sturgeon were observed at the air-water interface in unsealed tanks, or just below the lid in sealed tanks. Fin margins of dead individuals were perfused with blood, an indicator of oxygen deprivation (Jobling, 1995).

Growth

Across replicates, growth rates ranged in weight from 0.3% to 5.1% per day (Table 3). Sturgeon experienced positive growth in weight and length under all experimental conditions. Initial mean weights and lengths varied substantially among experiments; range was 10.94 to 69.20 g in weight and 14.59 to 26.60 cm in length. Absolute growth in weight was positively related to initial size (regression analysis; P<0.01); tanks with fish having initial mean weights greater than 50 g showed the highest absolute growth rates (>1.0 mg/d). Because initial size covaried with growth rate, initial weight was used as a covariate in statistical analyses of treatment effects.

Analysis of variance of instantaneous growth rate showed significant effects due to surface access and oxygen level (Table 4); temperature, replicate, and individual fish did not explain significant variance, although at 7 mg/L DO there was a trend for lower growth rates at 26°C than at 19°C (Fig. 2, Table 3). Mean growth rates were 2.9 times less at 3 mg/L (1.27%/d) than at 7 mg/L (3.62%/d). Sealed tanks showed consistently lower growth rates than those with surface access. The effect was greatest at 3 mg/L oxygen. Only 0.3%/d weight-specific growth was observed in the 19°C sealed tanks, and all fish perished before growth determinations could be made in the 26°C sealed tanks. Absolute growth in weight was significantly affected by surface access, temperature, surface access in combination with temperature interaction, and by oxygen level. Absolute growth rate was higher when surface access was allowed and at the higher DO level; absolute growth rate was inversely related to temperature.

Respiration

Respiration rates measured over the entire experiment ranged from 0.05 to 0.55 mg O_2/(g·h) (Fig. 3). Respiration rates were normally distributed for the high oxygen treatment with a mean of 0.245 ± 0.013

Table 3

Growth rates (mean ± standard error) of Atlantic sturgeon during the laboratory experiment. Growth rates in weight and length are instantaneous rates. Absolute growth rates in weight is presented under the heading mg/d. Experiments are labeled according to the temperature level and whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Dissolved oxygen (DO) levels, low and high, refer to prescribed levels of 3 mg/L and 7 mg/L, respectively. n = number of individuals in each tank. Rep. = replicate(s).

Experiment	DO level	Rep.	Growth rate in weight (per day)	mg/d	Growth rate in length (per day)	n
26°C unsealed	Low	1	0.023 ± .006	0.345 ± 0.094	~0	2
		2	0.013 ± 0.003	0.202 ± 0.056	~0	6
		3	0.006 ± 0.005	0.093 ± 0.062	0.003 ± 0.001	4
		4	0.029 ± 0.019	0.324 ± 0.192	0.003 ± 0.001	8
	High	1	0.037 ± 0.004	0.524 ± 0.076	0.010 ± 0.001	8
		2	0.037 ± 0.006	0.643 ± 0.116	0.012 ± 0.002	8
		3	0.036 ± 0.007	0.587 ± 0.112	0.012 ± 0.002	8
		4	0.036 ± 0.004	0.789 ± 0.117	0.015 ± 0.001	8
26°C sealed	Low	1	Lethal			0
		2	Lethal			0
	High	1	0.029 ± 0.001	2.220 ± 0.059	0.006 ± 0.001	6
		2	0.025 ± 0.001	2.015 ± 0.178	0.007 ± 0.001	6
19°C unsealed	Low	1	0.013 ± 0.002	0.185 ± 0.029	0.005 ± 0.001	7
		2	0.011 ± 0.003	0.129 ± 0.037	0.005 ± 0.001	7
	High	1	0.050 ± 0.005	0.721 ± 0.057	0.014 ± 0.001	8
		2	0.045 ± 0.002	0.719 ± 0.044	0.015 ± 0.001	8
19°C sealed	Low	1	0.003 ± 0.001	0.072 ± 0.030	0.004 ± 0.001	8
		2	0.003 ± 0.001	0.071 ± 0.031	0.004 ± 0.001	8
	High	1	0.028 ± 0.003	1.887 ± 0.253	0.009 ± 0.001	6
		2	0.031 ± 0.002	2.270 ± 0.197	0.008 ± 0.001	6

Table 4

Nested analysis of variance of surface access, temperature, oxygen level, replicate and individual effects on growth rate. Initial weight was used as a covariate in the analyses. Sealed refers to whether tanks were sealed or unsealed (unsealed tanks permitted access by sturgeon to surface water). Designated temperature and oxygen levels were 19°C and 26°C, and 3 mg/L and 7 mg/L, respectively. Factors in parentheses indicate the nesting procedure. For example "Oxygen (Sealed-Temperature)" refers to variance explained by oxygen level nested within combinations of surface access and temperature.

Type of variable	Variable	df	Sum of squares	Significance level (P)
Instantaneous growth rate in weight				
Covariate	Initial weight	1	0.3892	0.0001
Class variables	Sealed	1	0.0392	0.019
	Temperature (sealed)	2	0.0086	0.54
	Oxygen (sealed-temperature)	3	0.0981	0.0039
	Tank (sealed-temperature-oxygen)	7	0.0097	0.99
	Individual (sealed-temperature-oxygen-tank)	14	0.0077	0.99
Absolute growth rate in weight				
Covariate	Initial weight	1	0.0839	0.0001
Class variables	Sealed	1	0.0445	0.0001
	Temperature (sealed)	2	0.0523	0.0002
	Oxygen (sealed-temperature)	3	0.7734	0.0001
	Tank (sealed-temperature-oxygen)	7	0.0293	0.17
	Individual (sealed-temperature-oxygen-tank)	14	0.0194	0.92

mg O_2/(g·h). In relation to the high oxygen treatment, hypoxic oxygen treatment respiration rates were skewed towards lower rates with a mean of 0.174 ±0.016 mg O_2/(g·h). Two individual tank respiration rates for the hypoxic treatment were exceptionally high (Fig. 3). These data were measured at 0 hours from tanks at 19°C and 26°C and may have reflected an insufficiently long period of acclimation prior to the experiments. Therefore, we chose to exclude measures taken at 0 hours in the analysis of variance on respiration rates.

Respiration rates were significantly influenced by oxygen level (P=0.001), by the interactions between temperature and oxygen (P=0.04), and by the interaction among temperature, oxygen, and replicate (P=0.04). Mean respiration rates were 0.187 ± 0.012 and 0.247 ± 0.015 mg O_2/(g·h) under hypoxia and normoxia, respectively (Table 1). At high oxygen levels, 26°C respiration rates (mean=0.281 ±0.023 mg O_2/(g·h)) tended to be higher than 19°C respiration rates (mean=0.210 ±0.021 mg O_2/(g·h)). However, the converse was true at hypoxic levels; mean respiration rate at 26°C (0.136 ±0.027 mg O_2/(g·h)) was significantly lower than at 19°C (0.212 ±0.021 mg O_2/(g·h)). For all but the 26°C and hypoxic-level combination, replicate rates were similar. Respiration for the second replicate for the 26°C and hypoxic-level combination was substantially lower than other replicates that may have produced the significant interaction among temperature, oxygen, and replicate factors in the analysis of variance. In a procedure to reduce bias associated with deviations of actual inflow DO levels from those prescribed, an analysis of variance was conducted for which the inflow oxygen concentration was a covariate. After viariance associated with individual tank DO conditions was removed, the effect of oxygen level (high or low) remained significant (P=0.04).

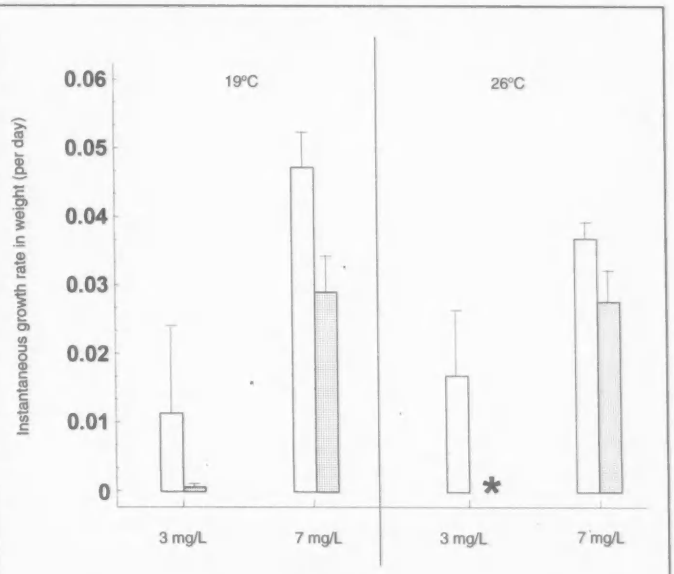

Figure 2

Effects of dissolved oxygen concentration on instantaneous growth rates in weight (per day) (mean ± 95% confidence interval) of young-of-the-year Atlantic sturgeon at two temperatures and different tank configurations. Stippled bars indicate treatments denying surface access. Replicate tanks were combined for each treatment level comination. The asterisk indicates that complete mortality occurred for that treatment.

Discussion

Juvenile Atlantic sturgeon were vulnerable to conditions of high temperature and low oxygen. In five out of six replicates (sealed and unsealed tanks combined) at 26°C and ~3 mg/L DO, all juveniles died. All sturgeon that died showed a perfusion of blood along the margins of their fins, indicative of oxygen deprivation (Jobling, 1995). Reduced oxygen levels resulted in a threefold reduction in growth rate and a 50% reduction in routine respiration rate. At 19°C, respiration rates were similar between hypoxic and normoxic treatments. But, at the 26°C hypoxic treatment, mean respiration rates dropped below 2 mg O_2/(g·h) and all sturgeon died. We speculate that these fish were unable to supply sufficient oxygen to their tissues at this level of reduced respiration.

Despite reduced survival and respiration in conditions of low dissolved oxygen, feeding continued and fish grew. Apparently, Atlantic sturgeon were able to reduce activity but still feed and allocate some energy to growth. In unsealed tanks, weight gain ranged from 1.1% to 2.9%, and from 3.6% to 5.0% body weight per day, at ~3 and ~7 mg O_2/L, respectively. Cech et al. (1984) also observed continued growth by juvenile white sturgeon (*Acipenser transmontanus*) (ca. 0.5 to 5 g) under conditions of hypoxia. Daily weight-specific growth rates of white sturgeon varied between 1.6% (15°C) and 2.9% (25°C) under normoxic conditions and between 0.6% (15°C) and 2.3% (25°C) under hypoxic conditions. Growth rates measured by Cech et al. (1984) under hypoxia were substantially higher than those that we ob-

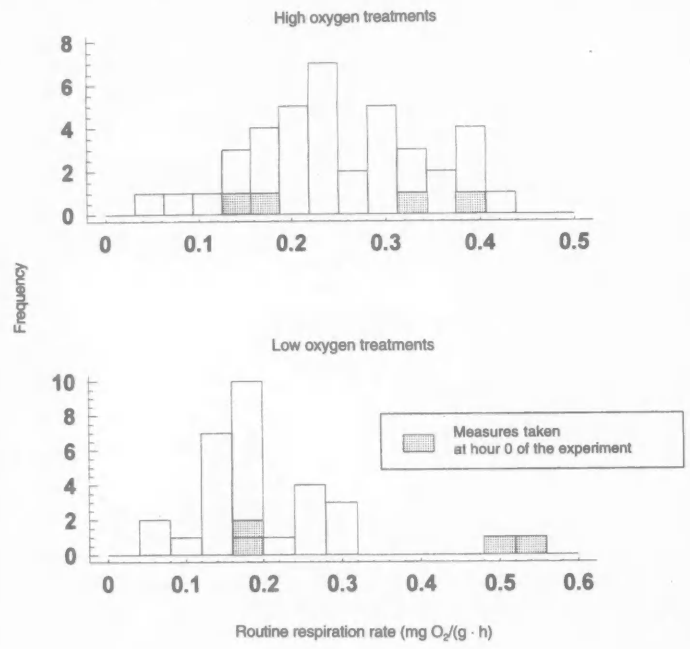
High oxygen treatments
Frequency
Low oxygen treatments
Measures taken at hour 0 of the experiment
Routine respiration rate (mg O2/(g · h)

Figure 3

Frequency histogram of respiration rates for young-of-the-year Atlantic sturgeon exposed to either high (7 mg/L) or low levels (3 mg/L) of dissolved oxygen. Measures taken at the initiation of the experiment (hour 0) are stippled.

served. This may be attributable to a higher designated oxygen level for hypoxic treatments (<5 mg/L), differences between the two species, or an ontogenetic effect. Juvenile white sturgeon were substantially smaller (initial weight 0.5 grams) than those used in our study (mean initial weight=23.7 grams).

Our study was unique in examining the effects of long-term hypoxia on routine metabolism. Other studies have examined the effects of hypoxia on sturgeon respiration in short-term respirometry studies (Table 5). Investigations on white sturgeon and Siberian sturgeon (*Acipenser baeri*) have indicated reduced rates of respiration under hypoxic conditions. An ontogenetic trend of decreasing routine metabolic rates with increased mass, which is typical in fishes, was also suggested in the comparison of studies. Metabolic rates under normoxic conditions ranged from 0.9 mg O_2/(g·h) (1–2 g fish) to 0.055 mg O_2/(g·h) (1800-g fish). Metabolic rates (0.2

Table 5

Summary of studies on hypoxia and routine metabolism for sturgeons. Oxygen concentrations and consumption rates have been converted to common units (mg O_2/L or mg O_2/(g·h) from reported units (e.g. mm Hg or µmol O_2/kg(g·h) for several of the studies. Wt = wet weight; Hyp = hypoxia treatment; Norm = normoxia treatment; Swim = velocities were provided in respirometer to induce swimming velocities; S = salinity; and T = temperature.

Species	Wt (g)	Treatments	Routine metabolism mg/(g·h)	S (ppt)	T (°C)	Study duration	Reference
Acipenser transmontanus	0.5–5	Hyp: 4.7 - 5.7 mg/L Norm: 6.8 - 8.2 mg/L	Not measured	0	15, 20, 25	30 d	Cech et al., 1984
A. baeri	1–2	High density Low density	0.3 to 0.5 0.4 to 0.9	0	22–24	2–12 h	Khakimullin, 1987
A. baeri	3–7	Routine Swim: 5–30 cm/sec	0.3 to 0.7 0.4 to 3.6	0	22–24	3 h	Khakimullin, 1988
A. oxyrinchus	12–69	Hyp: 2.5–4.4 mg/L Norm: 6.3–7.4 mg/L	0.1 to 0.2 0.2 to 0.3	1.8–2.5	19, 26	10 d	This study
A. transmontanus	950	Hyp: 1.7–6.3 mg/L Norm: 9.8 mg/L	~0 to 0.015 0.079	0	15	4.5 h	Burggren and Randall, 1978
A. baeri	1800	Hyp: 1.3–3.8 mg/L Norm: 8.2 mg/L	0.023 0.055	0	15	3.5 h	Nonnotte et al., 1993
A. transmontanus	2000	Hyp: 4.7–5.9 mg/L Norm: 7.7–8.9mg/L	0.090 0.098	0 0	18	24 h	Ruer et al., 1987

to 0.3 mg O_2/(g·h) and fish sizes (12 to 69 g) in our experiments were both intermediate within this range.

Surface behavior

In the nested growth and survival experiment, surface access influenced both growth and survival rates. Eliminating surface accesses in tanks reduced growth rates by ca. 35%, and fivefold at high and low levels of DO, respectively. The effects of denying surface access under "hypoxia" at 26°C was fully lethal within a 30-h period. In the 26°C hypoxic treatments that allowed surface access, the majority of juveniles survived the first 5 days of exposure, although they too eventually died.

Many fishes surface in hypoxic environments to convey relatively oxygen-rich water, located at the air-water interface, across their gills. In laboratory experiment, access to surface waters may have increased the effective level of DO above nominal levels, resulting in improved growth and survival. Alternatively, aerial respiration cannot be ruled out for sturgeon that are physostomous. Histological studies should be undertaken to investigate whether the swim bladder of Atlantic sturgeon contains a vascular structure, apart from the gas gland, which meets the criteria for an aerial respiratory organ. No such structure has been identified in any sturgeon species.

Reasons for decline of Atlantic sturgeon in Chesapeake Bay

We conclude that increased frequency of hypoxia in Chesapeake Bay during this century (Officer et al., 1984; Cooper and Brush, 1993) was detrimental to Atlantic sturgeon production. Recent water quality monitoring has shown that during summer months (mid-June through mid-September), temperatures >25°C and DO levels <4.0 mg O_2/L are prevalent in Chesapeake Bay benthic habitats (Breitburg, 1990, 1992; Phil et al., 1991). Our laboratory experiments showed that juvenile Atlantic sturgeon were less tolerant of summertime hypoxia than were other juvenile estuarine species. Young-of-the-year spot, *Leiostomus xanthurus* (total length 10–20 cm), survived long-term (>1 week) experimental exposure of 2.4–3.0 mg/L at 25°C, but 0.8–1.0 mg/L DO was fully lethal (Phil et al., 1991). Juvenile and adult hogchokers, *Trinectes maculatus* (Phil et al., 1991), and naked gobies, *Gobiosoma bosc* (Brietburg, 1992), can tolerate several-day periods of 0.5–1.0 mg/L DO.

Our laboratory experiments did not consider behaviors that can 1) reduce exposure to hypoxic waters and 2) compensate for reduced dissolved oxygen levels. Phil et al. (1991) and Brietburg (1992) have provided field evidence that fish will escape hypoxic conditions through local migrations. These include vertical or shoalward emigrations from hypoxic or anoxic bottom habitats. Following hypoxic events, bottom habitats are recolonized. Further, short-term episodic hypoxia may benefit bottom-feeding fish. Burrowing macrobenthic prey will emerge at DO levels <2 mg/L, increasing their vulnerability to predation by fish that can tolerate short-term excursions into hypoxic waters (Phil et al., 1992). If unable to escape hypoxic conditions, sturgeon may be able to compensate by either surfacing to exploit higher oxygen concentrations in surficial water or in the atmosphere or by adjusting their metabolic rate (e.g. through reduced swimming [Cech et al., 1984]).

Hudson River "strain" Atlantic sturgeon, used in our experiment, might have exhibited a different response to hypoxia than a strain native to Chesapeake Bay. The Hudson River rarely becomes hypoxic (Cooper et al., 1988). Therefore, Hudson River Atlantic sturgeon may not have been adapted to hypoxic conditions. An aquaculture study by Serov et al. (1988) on stellate sturgeon (*A. stellatus*) showed that heterozygosity in the LDH gene conferred survival advantages to hypoxia and high temperature. Therefore, it is conceivable that selection of Chesapeake Bay Atlantic sturgeon to hypoxic conditions could have occurred over several generations. However, because generation time is extremely high in Atlantic sturgeon (c.a. 29 years [Stevenson and Secor, 1996]) and because hypoxia increased rapidly during this century in the Chesapeake Bay, Chesapeake Bay Atlantic sturgeon may not have been able to recoup historical abundances by dint of selection to low-oxygen conditions. In addition, Hudson River Atlantic sturgeon juveniles >80 cm TL are known to visit Chesapeake Bay during summer months (Dovel and Berggren, 1983). Presumably, these fish could have adapted to Chesapeake Bay conditions. Serov et al.'s (1988) observation that water quality experienced by juveniles in culture influences genotypic frequencies has important implications for the use of hatchery-produced sturgeon in restoration programs and merits additional research.

Scientists and managers are now considering a restoration program for Atlantic sturgeon in Chesapeake Bay and elsewhere (St. Pierre, 1994; Secor, 1995). The feasibility of a sturgeon restoration program must address the same issues that led to the sturgeon's decline. If these conditions persist in Chesapeake Bay, a restoration program cannot be easily justified. Necessary conditions for population recovery must include increased population abundance, and improvement in the quality and size and number of essential habitats. Population abundance

can be increased by deliberately releasing artificially produced progeny (parentage from an outside population like the Hudson River population), by imposing a moratorium on sturgeon harvests, and by making efforts to reduce sturgeon taken as bycatch in other fisheries.

A critical and unresolved question is whether habitat quality remains sufficient at present in the Chesapeake Bay to support Atlantic sturgeon growth, survival, and reproduction. An encouraging finding has been a trend in improved water quality and macrobenthic production in Chesapeake Bay tributary nursery habitats, the apparent result of nutrient abatement programs (Dauer, 1995).

Acknowledgments

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Multiple population bottlenecks and DNA diversity in populations of wild striped bass, *Morone saxatilis*

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Abstract.—Striped bass, *Morone saxatilis*, in the Coos River, Oregon, are derived from natural colonists from San Francisco Bay, which in turn were intentionally transplanted from the Hudson River. Because of founder effects, this unusually well-documented colonization sequence should have resulted in diminished genetic variability in the penultimate and ultimate populations, which may have been further compounded in the Coos River population by subsequent drastic reductions in its abundance. To test whether these sequential bottlenecks reduced genetic diversity we surveyed both nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) variation in the Coos River population and in both populations along the historical pathway that led to its founding. There was no evidence of reduced nDNA diversity among these populations at the three loci examined. However, the number of mtDNA haplotypes revealed decreased from 8 in the original Hudson River population, to 5 in the San Francisco Bay population, to only 1 in the Coos River population. This pattern of conserved nDNA diversity and reduced mtDNA diversity is consistent with a recent population bottleneck. Coos River striped bass have shown increasing levels of pathological hermaphroditism. We speculate that the reduced genetic diversity of the Coos River striped bass population may have led to a depensatory cascade involving hermaphroditism that inhibited reproduction and recruitment, followed by increased levels of inbreeding as the population declined.

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Fishery Bulletin 96:614–620 (1998).

Population bottlenecks are often invoked to explain lower than expected levels of genetic diversity in wild populations of fishes (e.g. Bernatchez et al., 1989; Brown et al., 1992; Richardson and Gold, 1997), but rarely is there detailed information available on the degree and duration of the bottlenecks. Striped bass (*Morone saxatilis*) offer an exception because sequentially established populations (Fig. 1) in historical times have experienced unusually well documented bottlenecks.

Striped bass were introduced to the Pacific coast at San Francisco Bay in 1879 and 1882 (Stevens et al., 1987). The two plantings totaled approximately 430 individuals (132 in 1879; approximately 300 in 1882). All were yearlings collected in the Navesink and Shrewsbury rivers, New Jersey. The Navesink and Shrewsbury rivers are minor systems that do not support reproduction by striped bass and that are located near the mouth of the Hudson River; the transplants were almost certainly part of the proximal Hudson River striped bass population. The transplanted yearlings rapidly established a population in San Francisco Bay which reproduced in its two main tributaries: the Sacramento and San Joaquin rivers. The introduction of striped bass to San Francisco Bay has been viewed as one of the few highly successful introductions of non-native fishes (Raney, 1952); within 10 years of the original introduction striped bass were available in commercial quantities in California waters.

The first striped bass captured in Oregon waters were two adults taken in Coos Bay in 1914 (Morgan and Gerlach[1]). These fish were vagrants (or less likely, the offspring of vagrants) from the San Francisco Bay population, the only possible source along the Pacific coast. Since 1914, reproducing populations of striped bass became established in Oregon in the Coos, Coquille, Umpqua, Smith, and Siuslaw estuaries. Of these, the Coos River population was the largest and most studied.

[1] Morgan, A. R., and A. R. Gerlach. 1950. Striped bass studies on Coos Bay, Oregon in 1949 and 1950. Oregon Fish Commission Contribution 14, 31 p.

Figure 1
Colonization pathway of striped bass populations surveyed.

By the mid-1920s, striped bass were being commercially harvested in Coos Bay, and in 1945, annual landings from Coos Bay reached a high of 231,000 lb. The adult population also appeared to peak in 1945 at about 69,000 individuals (≥age-3), based on catch-per-unit-of-effort sampling. Pathological hermaphroditism was noted, but it was rare among Coos River striped bass during this period; Morgan and Gerlach[1] reported a 3% (n=124) incidence in 1950.

Since 1945, the Coos River striped bass population has crashed, whereas the incidence of hermaphroditism has increased dramatically. Between 1950 and 1975, population estimates of adults ranged from as many as 43,000 in 1963 to as few as 7800 in 1973. No adult population estimate is available for 1980, but in that year Moser et al. (1983) found 11 of 42 (26%) wild fish to be hermaphrodites. Population size of Coos River adult striped bass was not evaluated again until 1988 and 1989, when estimates of between 1000 and 3000 for both years were obtained. Estimates to date for the 1990s are of an adult population size under 1000. Furthermore, virtually no natural recruitment appears to be occurring (but supplemention is occurring through stocking of hatchery-produced offspring of San Francisco Bay broodstock). A standardized seine-haul survey of juvenile production begun in 1978 showed a decline in catch-per-unit-of-effort from 2.9 in 1978 to between 0.3 and 0.1 until 1986, and then only infinitesimal levels or zero through 1995. Recent estimates are that hermaphrodites make up 30% of the naturally produced adult population in the Coos River system (Reimers et al.[2]). Additionally, during 1993, an angling guide captured a hermaphroditic striped bass from the Umpqua River, the first reported from that system.

We hypothesized that Coos River striped bass would show reduced genetic diversity because both the history of the population's establishment and its subsequent demographics favored inbreeding. To test this hypothesis, we surveyed both nuclear DNA (nDNA) and mitochondrial DNA (mtDNA) variation in the Coos River population, the similarly non-native San Francisco Bay population (the source of the Oregon populations), and the source for the San Francisco Bay population, the Hudson River, New York. We also examined mtDNA variation in a second Oregon population (Umpqua River).

Methods

Coos River striped bass (both wild fish and fish that were originally hatchery-cultured) were captured in gill nets during spring 1993. These fish were distinguished on the basis of size; significant stocking of hatchery-cultured striped bass (age-0 only) did not begin until 1989. Only wild Oregon striped bass were used as broodstock until 1991, when broodstock from California were used. Umpqua River specimens were collected in 1992 by angling. San Francisco Bay samples were collected by means of gillnetting in the lower Sacramento and San Joaquin rivers during 1991 and 1992. Collections of striped bass from the Hudson River are described in Wirgin et al. (1990, 1993).

Total DNA was isolated from livers or blood by the CTAB method (Saghai-Maroof et al., 1984; Wirgin et al., 1990), phenol-chloroform extractions, and ethanol precipitations. To determine mtDNA haplotypes, DNAs were digested with *Acc* I, *Hind* III, and *Rsa* I, electrophoretically separated in 1.2% agarose gels, and visualized in Southern blot analyses by using ^{32}P

[2] Reimers, P. E., R. E. Bender, J. A. Johnson, T. Rumreich, D. J. Van Dyke, T. A. Confer, R. C. Smith, J. A. Hutado, and R. S. Boots. 1990. Tenmile-Coos-Coquille Fish District: a review of stocks of concern. State conservation department report, Oregon Department of Fish and Wildlife, 41 p.

Table 1

Genotypic frequencies for three single copy, nuclear DNA loci. Heterozygosity values in parentheses.

	Locus 25 *Dra* I				Locus 27 *Eco*R V				Locus 22 *Hinf* I			
Population	*N*	AA	AB	BB	*N*	AA	AB	BB	*N*	AA	AB	BB
Hudson River	35	0	11 (0.314)	24	123	6	42 (0.342)	75	80	47	24 (0.300)	9
San Francisco Bay	64	6	23 (0.359)	35	49	3	22 (0.449)	24	65	41	20 (0.308)	4
Coos River (wild)	27	1	12 (0.444)	14	32	3	14 (0.438)	15	34	11	9 (0.265)	14
Coos River (hatchery)	23	1	11 (0.478)	11	25	6	7 (0.280)	12	19	6	5 (0.263)	8

radiolabelled DNA probes (Feinberg and Vogelstein, 1983). Each of the three enzymes generates a diagnostic fragment which was used to characterize mtDNA major length-variant haplotypes (defined as differences of more than 100 base pairs; Wirgin et al., 1990). In addition, *Acc* I digestion revealed an informative, single base substitution. Probes were either highly purified mtDNA isolated from a single striped bass liver (Wirgin et al., 1990) or a gel-purified 1.7 kb PCR product containing the striped bass mtDNA control region (Wirgin et al., 1995). To determine nDNA genotypes, DNAs (10 µg) were digested with *Dra* I, *Eco*R V, and *Hinf* I, and analyzed in Southern blot analysis with the single copy probes developed from a striped bass genomic DNA library: DSB 25, DSB 27, and DSB 22, respectively (Wirgin and Maceda, 1991). Each of these enzyme-probe combinations revealed a single restriction site polymorphism with two alleles. Analysis of controlled laboratory matings demonstrated the Mendelian inheritance and nonlinkage of loci.

Genotypic frequencies derived from nDNA analysis were tested for deviations from Hardy-Weinberg equilibrium with the disequilibrium coefficient approach (Weir, 1990). Mitochondrial DNA haplotype diversity was calculated with the formula of Nei and Tajima (1981). Chi-square significance ($P<0.05$) of the differences between striped bass populations in nDNA allele frequencies and mtDNA haplotype frequencies was tested by using the randomization approach of Roff and Bentzen (1989).

Results

Nuclear DNA

Genotypic frequencies (Table 1) at two loci of samples from the Hudson River, San Francisco Bay, and Coos River (wild and hatchery) did not deviate significantly ($P>0.05$) from Hardy-Weinberg equilibrium; however, locus 22 did differ significantly from Hardy-Weinberg equilibrium for the Coos River wild ($P<0.01$) and hatchery ($P<0.05$) samples. Allelic frequencies for the three nDNA loci did not differ significantly ($P>0.05$) between the Hudson River and San Francisco Bay collections. Of the three nDNA loci, only locus 22 differed significantly in allelic frequencies between the San Francisco Bay and Coos River collections ($\chi^2=19.21$; $P<0.0001$).

Mitochondrial DNA

Mitochondrial DNA haplotypic diversity (based on mtDNA length variants) showed a clear pattern of reduction (0.810 to 0.0) among the striped bass populations along the historical path that led to and includes the wild Coos River population (Table 2). The number of mtDNA haplotypes revealed decreased from 8 among Hudson River specimens to 5 in the San Francisco Bay collection, to 2 in the Umpqua, and 1 in the wild and hatchery-cultured Coos River samples. The third most common haplotype (C-1) found in the Hudson River collection (17%) was observed in the great majority of San Francisco Bay specimens (81%) and in all Coos River specimens. Also, the three least common haplotypes in Hudson River striped bass were those absent in striped bass from San Francisco Bay. Mitochondrial DNA haplotype frequencies were significantly different between the Hudson River and San Francisco Bay samples ($\chi^2=71.47$; $P<0.0001$) and between the San Francisco Bay and Coos River samples ($\chi^2=8.21$; $P<0.05$).

Discussion

Extensive allelic surveys of Atlantic coast striped bass have shown extreme monomorphism at the pro-

Table 2

Mitochondrial DNA composite haplotype frequencies (letters represent length polymorphisms; numerals represent site polymorphisms; percentages in parentheses) and genotypic diversity indices.

Population	*N*	Haplotype								Genotypic diversity
		A-1	A-2	B-1	B-2	C-1	C-2	D-1	D-2	
Hudson River	110	3 (0.03)	2 (0.02)	25 (0.23)	7 (0.06)	19 (0.17)	32 (0.29)	17 (0.15)	5 (0.04)	0.810
San Francisco Bay	63			4 (0.06)	4 (0.06)	51 (0.81)	2 (0.03)	2 (0.03)		0.340
Coos Bay (wild)	38					38 (1.0)				0.0
Coos Bay (hatchery)	27					27 (1.0)				0.0
Umpqua River	12					11 (0.92)	1 (0.08)			0.167

tein level both within and among populations (reviewed in Waldman et al., 1988). For example, Otto (1995) reported mean heterozygosity levels of Atlantic striped bass of approximately 1.0%, and 0.75% for the Hudson River population. Very low genetic diversity for Atlantic coast striped bass has also been shown by several mtDNA studies (Chapman, 1990; Wirgin et al., 1990, 1993; Waldman and Wirgin, 1994). For example, Wirgin et al. (1990) estimated the proportion of nucleotides that differed for the most divergent individuals among mid-Atlantic striped bass stocks at 0.0004, one of the lowest values for any animal species. What mtDNA variation does exist in striped bass primarily is length, rather than site variation (Waldman and Wirgin, 1995). Four mtDNA major length variants have been found in striped bass from the Hudson River (Wirgin et al., 1990, 1993; Waldman and Wirgin, 1994).

Thus, the substrate of genetic variation available among striped bass from the Hudson River and other Atlantic coast estuaries was extremely low in comparison with most fishes (e.g. Waldman et al., 1996). From this unusually narrow gene pool some 430 or so yearlings were collected and transplanted in 1879 and 1882 to San Francisco Bay. It is not known how many of the female yearlings survived to reproduce as founders of all Pacific coast striped bass, but about 215 represents an approximate upper limit (assuming an unrealistic 100% survival rate), and 5 the lower limit, given the 5 haplotypes detected. Estimates of annual expectation of death from natural causes of the San Francisco Bay striped bass population obtained during a period of exploitation (summarized in Westin and Rogers[3]) ranged between 0.31 and 0.12, and averaged about 0.2. Moreover, female striped bass have variable maturation schedules (Berlinsky et al., 1995); in San Francisco Bay, it has been found that females mature at ages 4 and 5 (Stevens et al., 1987). Therefore, a more reasonable estimate for the number of transplanted females that survived to found the San Francisco Bay striped bass population is about 100.

Striped bass then appeared in Coos Bay some 35 years after their introduction to San Francisco Bay. It is not possible to determine the number of founders of the Oregon populations nor their initial genetic makeup. Present Oregon striped bass are restricted to mtDNA length haplotype C. It is not known what the mtDNA haplotype frequencies of the San Francisco Bay stock were circa 1915, but if their present haplotype frequencies are used as an approximation, then the chance of a single female founder having a haplotype other than the C haplotype is only 16%. We believe that given the historical scarcity of striped bass in north Pacific coastal waters (Forrester et al., 1972) and the concordance between the dominant haplotype of the San Francisco Bay stock and the single (major length variant) haplotype of the Coos River and Umpqua River stocks, it is reasonable to assume that the Oregon populations were founded by one or a very low number of female striped bass with the C-haplotype.

Founding of the Oregon striped bass populations by a limited number of females from California, following the initial bottleneck of transplantation from the Atlantic, would have resulted in a greatly reduced level of genetic variation in comparison with the

[3] Westin, D. T., and B. A. Rogers. 1978. Synopsis of biological data on the striped bass, *Morone saxatilis* (Walbaum) 1792. Technical Report 67, Graduate School of Oceanography, Univ. Rhode Island, 154 p.

Hudson River stock. However, genetic variation may have been pared further, i.e. the subsequent history of the Coos River population suggests that some of the demographic and life history factors that contribute to low levels of genetic variation among native populations of striped bass were pronounced in the Coos River population.

The Coos River population has experienced its own bottleneck; recent estimates suggest a reduction in its order of magnitude from 10^4 to 10^3 or 10^2. Fluctuating levels of annual spawning success also reduce the effective population size (N_e). Over generations N_e is approximated by the harmonic mean of each generation and strongly reflects periods of low abundance (Crow and Kimura, 1970). Many striped bass populations are sustained by occasional, extremely successful or "dominant" year classes (Raney, 1952). Dominant year classes have been rare but important for the Coos River population, occurring in 1940 and 1958 (McGie and Mullen[4]).

Other factors that may have contributed to a reduced N_e for the Coos River population are intrinsic to all populations of the species. Among these is skewed sex ratios. Males greatly outnumbered females on the Coos River spawning grounds (Morgan and Gerlach[1]). Estimates of male to female ratios on spawning grounds of other systems range from about 10:1 to 100:1 (Chapman, 1990). Another factor is variance in progeny production among females, i.e. nonrandom family size (Gall, 1987). Large female striped bass can produce on the order of 10^6 eggs per year. Because of variable environmental conditions within a spawning season, some cohorts of eggs may show low or no survival whereas other cohorts may flourish (Dey, 1981; Secor and Houde, 1995). Thus, inordinate success by a few females would cause particular genotypes to be overrepresented (Chapman, 1990).

The significant difference in allele frequencies for nDNA locus 22 between the San Francisco Bay and Coos River collections indicates either a founder effect or subsequent genetic drift. Also, the deviation from Hardy-Weinberg equilibrium of one of the three loci in the Coos River population is suggestive of small N_e or some other violation of the assumptions that lead to Hardy-Weinberg frequencies (Weir, 1990). In general, however, it appears that nDNA diversity was not strongly affected by the multiple bottlenecks that the Oregon populations experienced. In contrast, we have shown a stark decrease in mtDNA diversity. Our findings concerning nDNA and mtDNA diversity in Oregon striped bass are congruent with their having experienced a recent population bottleneck. A single breeding pair of diploid animals contains four nuclear genomes and one transmissible mtDNA; thus, a population that goes through an extreme bottleneck can lose all of its mtDNA; variability while still retaining a significant fraction of its nuclear variability (Wilson et al., 1985). A pattern of highly reduced mtDNA diversity and little altered nDNA diversity is consistent with a recent and unprolonged population bottleneck, as we hypothesize to have occurred during the establishment and history of the Coos River striped bass population.

There is an intriguing inverse relationship between genetic diversity (reflected in mtDNA) of the striped bass populations investigated and the frequency of hermaphroditism. Inbreeding depression has been firmly associated with detrimental effects in captive vertebrate populations (e.g. Kincaid, 1976, Laikre and Ryman, 1991), and recently, strong evidence of reduced fitness and reproductive impairments due to inbreeding depression in wild vertebrates has emerged (e.g. Jimenez et al., 1994; Keller et al., 1994; O'Brien, 1994).

Moser et al. (1983) investigated the phenomenon of hermaphroditism in Coos River striped bass in some detail. Protandry was suspected because young hermaphrodites had ripe, motile sperm and immature eggs, whereas older hermaphrodites (ages 7 to 10) had normal appearing eggs and only small patches of testes. Reproductive impairment of older hermaphrodites was evident. Hermaphrodites with small testes and large ovaries showed annual accretions of eggs and one or more ovarian ducts blocked by adhesions. Each egg mass, representing previous spawning seasons, became progressively more degenerated toward the interior of the gonad. Moser et al. (1983) also found that the oldest hermaphrodites had more constricted stomachs and intestines and more swollen abdomens than normal prespawning females. The four oldest hermaphrodites, 10 years old, had retained their eggs for up to 5 years. Also, it is possible that the absence of hermaphrodites among striped bass greater than 10 years of age (n=7) indicates earlier mortality of hermaphroditic individuals, perhaps as a consequence of numerous annual egg mass accretions.

We are aware of only a single observation of hermaphroditism among Atlantic coast striped bass. Westin (1978) reported one hermaphrodite among wild individuals from Chesapeake Bay that were sacrificed after being held in captivity for one year. However, in addition to surveying Coos River striped bass for evidence of hermaphroditism, Moser et al. (1983) also examined striped bass from San Francisco Bay. Of more than 500 individuals, two were hermaphrodites. Thus, hermaphroditism in striped bass appears to be exceedingly rare in native, out-

[4] McGie, A. M., and R. E. Mullen. 1979. Age, growth, and population trends of striped bass, *Morone saxatilis*, in Oregon. Oregon Department of Fish and Wildlife Information Report Series, Fisheries 79-8, 57 p.

bred populations, barely detectable in a non-native, outbred, but somewhat genetically constrained population, and pronounced in a non-native, inbred population. Moreover, the inverse association between abundance and hermaphroditism of the Coos River population suggests (but does not demonstrate) that a depensatory relationship exists because of these factors. That is, demographic influences that continued to reduce genetic diversity of the Coos River population may have promoted this pathological reproductive response, which then hindered reproduction, further reducing abundance and leading to higher levels of inbreeding.

Furthermore, no strong competing hypotheses have emerged to account for hermaphroditism of the Coos River striped bass stock. Chemical contamination is one conceivable cause. However, the Hudson River—the original source of Coos River striped bass—is a heavily polluted estuary, yet hermaphroditism has not been observed in its population. Also, the Coos River is home to American shad (*Alosa sapidissima*), similarly transplanted from the Atlantic (in 1871 to the Sacramento River; Mansueti and Kolb, 1953). In its native east coast rivers, including the Hudson River, American shad overlap with striped bass both spatially and temporally on their spawning runs. Nonetheless, whereas the Coos River striped bass population has approached extinction, its American shad population is flourishing.

It is clear that populations of striped bass in Oregon would benefit from broader genetic diversity (although there is considerable controversy concerning maintenance of non-native fish populations; e.g. Courtenay, 1995). If perpetuation of the Coos River population is desired, consideration should be given to the introduction of striped bass to Oregon waters from one or more additional Atlantic coast stocks. A combination of intention and serendipity resulted in the establishment of striped bass in California and then Oregon; however, the ultimate effect was to promulgate northern, hypothermal, nonmigratory populations from individuals originally obtained from a midlatitude, mesothermal, migratory population. There is some evidence that striped bass from northern latitudes are better adapted to the ambient environmental conditions of those latitudes (Conover, 1990). We suggest that Atlantic coast striped bass from northerly latitudes such as the Canadian Maritimes would be more preadapted to Oregon habitats.

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Can scales be used to sex winter flounder, *Pleuronectes americanus*?

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We tested the accuracy of a technique to rapidly determine the sex of mature winter flounder, *Pleuronectes americanus*, in the field without sacrificing individuals. Although a number of techniques have been developed for sexing fish by examining reproductive anatomy (Moen, 1959; Driscoll, 1969; Martin et al., 1983; Ross, 1984), they are not well suited for easy and rapid determinations in the field: External characteristics, such as features of the urogenital region (Sigler, 1948; McComish, 1968; Flickinger, 1969; Lebeau and Pageau, 1989) or body shape (Snow, 1963), have been successfully applied in the field for other species but are not applicable to winter flounder which exhibit no obvious sexual dimorphism. Some studies have suggested that male and female winter flounder can be differentiated by the texture of the scales on the blind side; males allegedly have ctenoid scales which feel rough, whereas females allegedly have cycloid scales which feel smooth (Perlmutter, 1947; Lux and Porter, 1963). Unfortunately, the literature is inconclusive and none of the studies have carefully tested the relationship of texture as related to scale type and sex. MacPhee (1978) citing Norman (1934) claimed that scales on the blind side of males are ctenoid rather than cycloid when, in fact, Norman stated that for the species in general the scales are ctenoid on the ocular side and cycloid on the blind side.

Methods

From March through September, 1989, winter flounder were collected with an otter trawl in New Jersey waters. Fish were collected at 14 inshore sites in Raritan and Sandy Hook Bays (Phelan, 1992) and 22 offshore sites 22.2 km east of Sandy Hook (Studholme et al., 1995). Fish were measured to the nearest millimeter total length. Using the method described by Lux and Porter (1963), we palpated the blind side of the caudal peduncle noting either roughness (males) or smoothness (females). The fish were then dissected to determine (visually) maturity and sex. All immature fish were eliminated from the study. When possible, a sample of ten or more scales was taken from the palpated area. In the laboratory, the scales were examined with a dissecting microscope to determine their type and relation to texture.

Results and discussion

A total of 730 mature fish, ranging from 12.9 to 39.7 cm, were examined. External palpation resulted in a significantly higher (χ^2=51.528, P<0.001) sex ratio (females to males) of 2.7:1 than the actual ratio of 1.2:1 (Fig. 1). The difference in the ratios was due primarily to males being identified as females. Forty six percent (155 of 332) of the

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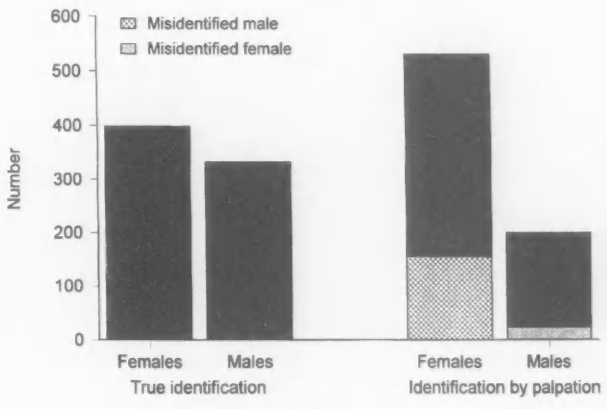

Figure 1
Number of female and male winter flounder (*Pleuronectes americanus*) identified by gonadal inspection and palpation of the blind side scales.

Table 1

Sex ratio of winter flounder as determined by external palpation and gonad inspection.

Sex ratio (female:male)	Method	Number of fish	Location	Source
2.5:1	External	3711	New England and New York	Perlmutter, 1947
2.3:1	External	601	Rhode Island	Saila, 1961
2.6:1	External	1431	New England	Lux and Porter, 1963; Lux, 1969
2.3:1	External	12,151	Massachusetts	Howe and Coates, 1975
1.5:1	Internal	940	Rhode Island	Saila, 1962
1.2:1	Internal	1569	Rhode Island	Berry et al., 1965
1:1	Internal	227	Newfoundland	Kennedy and Steele, 1971
1:1	Internal	1465	Massachusetts	Haedrich and Haedrich, 1974

males were misidentified, and six percent (23 of 398) of the females were identified as males. Similar differences between sex ratios derived from palpation of the scales and from gonadal inspection have been reported in the literature (Table 1). In the four studies that used palpation to determine sex, ratios ranged from 2.3 to 2.6:1 compared with ratios of 1:1 to 1.5:1 when gonads were used.

Scales were collected and examined from 672 of the 730 fish. Sex ratios for this subset also differed significantly (χ^2=44.203, P<0.001) between the two sexing methods: 2.5:1 for palpation and 1.2:1 for gonadal inspection (Fig. 2). Individual fish exhibited either cycloid (479 fish) or ctenoid (199) scales, a finding that differs from Norman's (1934) observation that scales on the blind side were cycloid. Female fish exhibited primarily cycloid scales (Fig. 2) which were present on 352 (98%) of the 361 females examined. Scale type for male fish, however, was variable; 120 (39%) fish exhibited cycloid scales and 191 (61%) ctenoid (Fig. 2). Discrepancies between texture determinations and scale type (observer error) occurred in 33 (5%) of the fish examined (Fig. 2).

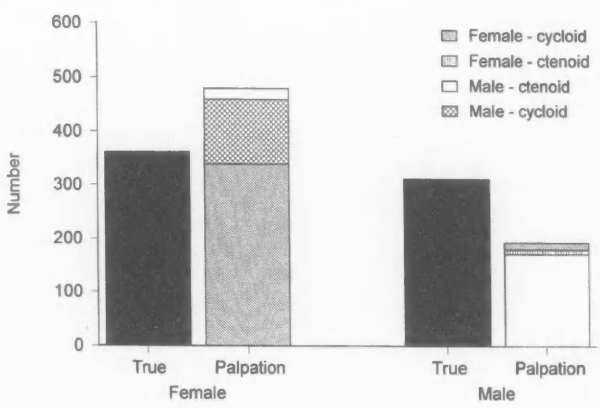

Figure 2

Number of female and male winter flounder (*Pleuronectes americanus*) identified by gonadal inspection and palpation in relation to scale type.

It is therefore apparent that the use of texture according to scale type for sexing winter flounder (Perlmutter, 1947; Lux and Porter, 1963; MacPhee, 1978) is not accurate, resulting in a significantly female-biased sex ratio.

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Evaluation of toxicity of oxytetracycline on growth of captive nurse sharks, *Ginglymostoma cirratum**

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Validation of age estimates derived from calcified structures is an essential component of all fish age and growth studies (Beamish and McFarlane, 1983). In elasmobranchs, age validation is accomplished through injection of tetracycline antibiotics, particularly oxytetracycline hydrochloride [OTC] (Cailliet, 1990). At a standard dosage level of 25 mg/kg body weight (BW), OTC is deposited at sites of active calcification and produces vivid, enduring marks in dorsal-fin spines and vertebral centra (Holden and Vince, 1973; Smith, 1984; Beamish and McFarlane, 1985; Branstetter, 1987; Brown and Gruber, 1988; Natanson and Cailliet, 1990; Kusher et al., 1992; Natanson, 1993; Walker et al.[1]). The location of these fluorescent marks can then be examined to determine if the structure in question accurately reflects age. Such OTC treatment is generally considered benign, yet few scientists have directly examined the potential toxicity of this compound to elasmobranchs. However, if OTC injection alters the growth or health of treated elasmobranchs, its value as a chemical marker for age validation may be severely compromised. Thus, studies on the toxicity of OTC and other potential chemical markers (Gelsleichter et al., 1997) are essential for the improvement of elasmobranch ageing biotechnology.

Chemical toxicity associated with OTC treatment has been well documented in several teleost ageing studies. For example, injection of, or immersion in, OTC at recommended dosage levels (Beamish and McFarlane, 1983) has been reported to produce lethargy, behavioral abnormalities, and mortality in treated specimens (Schmitt, 1984; Wilson et al., 1987; Marking et al., 1988; Monaghan, 1993; Bumguardner and King, 1996). In contrast, Tanaka (1990) reported that various dosage levels of OTC (20–80 mg/kg BW) did not significantly affect growth rates of injected Japanese wobbegongs (*Orectolobus japonicus)* or swell sharks *(Cephaloscyllium umbratile).* Unfortunately, no other studies have investigated the possible implications of OTC treatment in elasmobranchs and, thus, they remain largely unclear.

The goal of the present study was to evaluate the effect of OTC treatment on the growth rate of captive nurse sharks, *Ginglymostoma cirratum*. The potential effect of OTC injection on nurse shark health is also discussed on the basis of serologic and hematologic observations.

Materials and methods

Nine age-0 and age-1 *G. cirratum* were collected in the Florida Keys and transported to the laboratory, where they were maintained in outdoor circular tanks (capacity ranging from 3,200 to 12,000 L). The experimental tanks can operate as either open or recirculating systems and were subjected to natural photoperiod and temperature

[1] Walker, T. I., R. A. Officer, J. G. Clement, and L. P. Brown. 1995. Southern age validation: Part I—Project overview, vertebral structure and formation of growth increment bands used for age determination. Final Report to the Fisheries Research and Development Corporation, FRDC Project 91/037. Department of Conservation and Natural Resrouces, Queenscliff, Victoria, Australia.

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regimes. After an acclimation period of two weeks, all animals were sexed, measured (stretched total length; STL), weighed, and tagged with rototags for individual identification. Sharks were divided into two groups: an OTC group (n=5; mean STL (±SE)=62.6 ± 3.62 cm; mean weight (±SE)=1.7 ±0.36 kg) and a control (CO) group (n=4; mean STL=51.2 ±2.09 cm; mean weight = 0.9 ± 0.10 kg). All nine animals were injected in the lateral musculature with an elasmobranch Ringer's solution vehicle (Forster et al., 1972) which, for the OTC group, contained OTC at a dosage level of 25 mg/kg body weight (BW). Following the injections, all nurse sharks were returned to the experimental tanks for captive maintenance over a 7-month period.

During the experimental period, all sharks were measured, weighed, and examined for external lesions on a monthly basis. In addition, the general condition of all sharks was evaluated and recorded in terms of behavioral abnormalities or signs of distress. All animals were fed three times per week ad libitum with Atlantic thread herring, *Polydactylus oligodon,* or sardine, *Sardinella aurita*.

Toxicity of OTC on nurse shark growth was evaluated by comparing the mean growth rate (%BW/d) of control and OTC-injected *G. cirratum*. In addition, blood samples were obtained from all specimens at the end of the experimental period and subjected to white blood cell (WBC) and serologic parameter analyses. Afterwards, all remaining specimens were anesthetized with 1 g/L tricaine methanesulfonate (MS-222) and sacrificed by severing the spinal cord. Necropsies were performed for all specimens to assess general animal health.

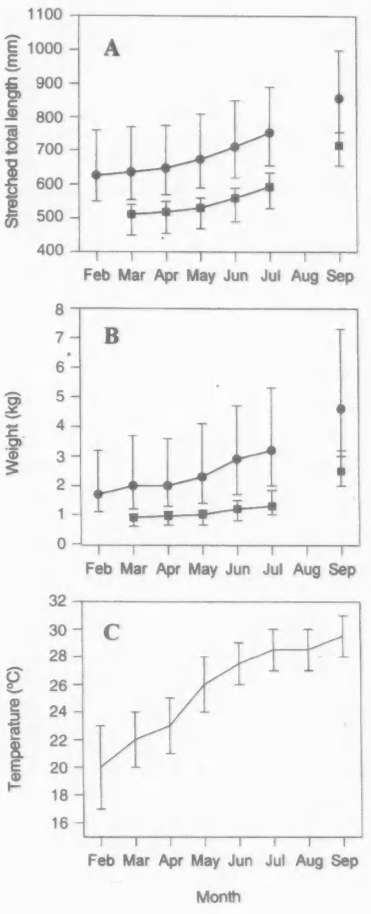

Figure 1

Mean monthly growth (± SE) in **(A)** length and **(B)** weight for nurse sharks in the OTC (●, n=5) and control (■, n=4) groups; **(C)** shows the monthly temperature ranges and midpoints in the experimental tanks.

Results

All nurse sharks survived the experimental period without any apparent behavioral complications. All grew in length (Fig. 1A) and weight (Fig. 1B) while exposed to identical temperature fluctuations (Fig. 1C). No significant differences in growth rates between control and OTC groups were observed (t-test, P<0.05, Table 1).

Observations on serum chemistry also indicated little difference between groups, except that both lactate dehydrogenase (LDH) and aspartate aminotransferase (AST) were significantly greater in OTC-injected animals (t-test, P<0.05, Table 2). Differential WBC counts indicated no significant difference between control and OTC groups (t-test, P<0.05; Table 3). Both serologic and hematologic

Table 1

Growth rates (expressed as %BW/d) of nurse sharks in the control and oxytetracycline-treated (OTC) groups. Body weights (BW) are in kg.

Group	n	Initial BW (Mean ± SE)	Final BW (Mean ± SE)	Growth rate (Mean ± SE)
Control	4	0.88 ± 0.10	2.52 ± 0.29	0.91 ± 0.11
OTC	5	1.70 ± 0.38	4.64 ± 0.73	0.79 ± 0.11

parameters were comparable with earlier observations by Stoskopf (1993) for captive *G. cirratum*.

Discussion

Tanaka (1990) determined that OTC injections at dosage levels from 20 to 80 mg/kg BW did not adversely affect growth or cause mortality in Japanese wobbegongs (*O. japonicus*) or swell sharks (*C. umbratile*). In agreement, the present study indicates no adverse effect of OTC treatment on the growth rate of injected *G. cirratum*. Therefore, continued use of OTC injection is still supported as an effective, nontoxic method for determining vertebral growth-band periodicity. In addition, OTC remains the superior chemical marker for elasmobranch age validation in comparison with calcein, which appears highly toxic at similar dosage levels (Gelsleichter et al., 1997).

Although OTC does not appear to affect short-term growth, high serum LDH and AST in OTC-injected *G. cirratum* may suggest that it can be hepatotoxic. High activities of LDH and AST are commonly used in the diagnosis of toxicant stress and hepatocellular injury, when these enzymes are leaked from damaged liver cells (Zimmerman et al., 1965; Racicot et al., 1975; Krajnovic-Ozretic and Ozretic, 1987). Unfortunately, the diagnosis of toxicant stress in elasmobranchs with enzyme activity levels has not been well investigated. In addition, serial blood sampling of injected animals prior to and after injection is necessary for an appropriate evaluation of serologic data. Consequently, interpretation of these data is speculative, yet may still indicate a harmful effect of OTC on elasmobranch physiology and thus require further investigation.

Hepatic dysfunction is a common repercussion of OTC treatment in vertebrates. In several species, OTC administration causes acute hepatocellular injury that is often associated with intracellular fat deposition and cytoplasmic alterations (Weinstein, 1970; Hennigar and Gross, 1977). However, these effects are usually associated with repeated exposure to dosage levels far greater than those used in fish age validation studies (Lepper, 1951; Sborov and Sutherland, 1951). In addition, elasmobranch liver cells regularly contain large deposits of intracellular fat in their normal state. Nevertheless, this standard information may lend some credence to observations on increased LDH and AST in treatment group specimens. Clearly, future studies on OTC toxicity should investigate other characteristics of health that are less conspicuous than animal growth or survival.

In conclusion, the results of the present study indicate that OTC treatment does not produce short-term effects on *G. cirratum* growth that may complicate age validation. However, minor tangential evi-

Table 2

Serologic parameters of nurse sharks at the end of the experimental period after injection with oxytetracycline hydrochloride (OTC) or vehicle at a dosage of 25 mg/kg body weight ; BUN = blood urea nitrogen; ALK P = alkaline phosphatase; LDH = lactate dehydrogenase; AST = aspartate aminotransferase; ALT = alanine aminotransferase. Values are means ± SE. The values marked with an asterisk are significantly different from control at $P < 0.05$.

	Groups	
Serologic parameter	Control (n=4)	OTC (n=5)
Glucose (mg/dL)	16.2 ± 0.86	18.0 ± 0.63
Sodium (mM/L)	272.7 ± 1.93	275.4 ± 1.63
Potassium (mM/L)	5.45 ± 0.10	5.47 ± 0.08
Chloride (mM/L)	260.0 ± 2.71	261.0 ± 1.48
CO_2 (mM /L)	7.7 ± 0.25	7.2 ± 0.20
BUN (mg/dL)	832.0 ± 12.17	811.6 ± 6.22
Creatinine (mg/dL)	0.10 ± 0	0.16 ± 0.02
Uric acid (mg/dL)	0.12 ± 0.03	0.18 ± 0.05
Calcium (mg/dL)	17.3 ± 0.28	17.8 ± 0.24
Phosphorus (mg/dL)	4.12 ± 0.17	4.14 ± 0.12
Total bilirubin (mg/dL)	0.1 ± 0	0.1 ± 0
ALK P (U/L)	33.5 ± 2.60	54.6 ± 9.79
LDH (U/L)	863.5 ± 122.9	1810.8* ± 371.7
AST (U/L)	24.7 ± 3.77	54.6* ± 9.35
ALT (U/L)	19.7 ± 1.25	23.2 ± 1.71

Table 3

Differential white blood cell counts of nurse sharks at the end of the experimental period after injection with OTC or vehicle at a dosage of 25 mg/kg BW; % WBC is the proportion of all blood cells that are white. Values are means ± SE.

Group or individual	n	Granulocytes (%)	Lymphocytes (%)	Monocytes (%)	Thrombocytes (%)	% WBC
Control	4	21.4 ± 2.6	51.1 ± 2.0	1.4 ± 0.3	26.1 ± 1.5	12.0 ± 0.6
OTC	5	22.4 ± 3.0	50.3 ± 3.0	1.9 ± 0.6	25.4 ± 1.9	11.2 ± 0.8

dence suggests that OTC may be hepatotoxic, affecting animal health over longer periods of time. Thus, additional studies on OTC toxicity may have important implications for long-term maintenance of marked elasmobranchs.

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Electrotaxis in American lobsters, *Homarus americanus*, and its potential use in sampling early benthic-phase animals

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The American lobster, *Homarus americanus*, fishery is an important part of the economy in New England and eastern Canada. A reliable predictor of recruitment to this fishery would be useful in stock assessments and economic planning, yet no such predictors are available. The best time for a prerecruit survey is just after the stage-4 postlarva (approx. 5-mm carapace length) settles from the plankton to the benthos, after high larval mortalities have established the size of the year class, but early enough in the growth cycle to allow prediction of recruitment 4–6 years before lobsters are harvested. Unfortunately, this is also the period when lobsters are most difficult to capture. Stage-4 lobsters prefer to settle into cobble-sized rock substrate, often several layers thick, where they remain until they begin to enter commercial traps at a carapace length of about 40 mm (Lawton and Lavalli, 1995). Sampling this "early benthic phase" (EBP) of lobsters is laborious and costly. A team of divers must turn individual rocks and capture escaping animals with suction devices (e.g. Hudon, 1987, Wahle and Steneck, 1992). This method is too time consuming to permit synoptic prerecruit surveys such as are conducted for groundfish. Consequently, we sought a more efficient sampling method for EBP lobster stocks along the coast of Nova Scotia, Canada.

Several previous studies suggested that electrofishing may be a useful approach. Saila and Williams (1972) developed an electric trawl system that increased catches of commercial-size American lobsters. Stewart (1974) described the effects of electric fields on the Norway lobster (*Nephrops norvegicus*), including an induced avoidance behavior that caused animals to leave their burrows. Phillips and Scolard (1980) developed an electrofishing apparatus for juvenile rock lobsters (*Panuliris cygnus*) which looked promising, although it caught a size range similar to that taken by traps. Our approach was fundamentally different from these studies in that we intended to develop a sampling "quadrant" which electrified a small area (<1 m^2) of the substrate and took advantage of electrically induced behavior observed in our preliminary laboratory experiments. This paper presents results from these experiments and subsequent trials with several potential electrode arrangements and suggests avenues for further development.

Methods

Preliminary behavioral experiments were conducted in tanks of various sizes without shelters or substrate to determine if electrotaxis could be induced in lobsters and, if so, what pulse lengths and voltages would be most effective. Lobsters ranging in size from 5–50 mm carapace length were subjected to a wide range of electrical stimulation including voltages from 10 to 100 V and pulse frequencies from 2 to 200 Hz. Pulse lengths were varied independently of frequency during these observations, but it quickly became obvious that a square wave form (pulse duration 50% of cycle length) with a relatively high frequency was most effective in inducing the desired response. Consequently, all experiments with different electrode configurations and cobble shelters were conducted at a DC pulse frequency of 100 Hz, pulse duration of 20 milliseconds, and an input voltage of 50 V. All these experiments were also conducted in a 1.5 m^3 tank (1 m × 2 m × 0.75 m), large enough so that the walls did not distort the relatively localized electric currents produced by the apparatus. The tank was filled with sand to a depth of 10 cm, and a group of 15 cobble-size rocks (average weight 2.5 kg) of various shapes obtained from known lobster habitat were placed in the central area of the tank so that they were several layers deep and entirely contained by a 0.35 m^2 quadrant. Indirect overhead fluorescent lighting was adjusted to the natural day length. The tank was kept filled

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with 15°C seawater with a continuous flow-through system. Three EBP animals ranging from stage 4 to stage 8 (5–10 mm carapace length) were used in each trial, which is within the range of naturally occurring densities. Each animal was used only once. At least 24 hours before each trial the experimental animals were chosen randomly from a previously unused group kept in 15°C flow through holding trays. The animals were released directly above the cobble (into which they always disappeared within a few seconds) and allowed to acclimate overnight. The released animals almost always remained within the rock pile and were seen on the surrounding sand only on rare occasions. After each trial, all rocks were removed from the tank, uncaptured animals were recovered, and the rocks were replaced haphazardly. This procedure produced a different configuration of burrowing locations and shelters for each trial and simulated the varied cobble habitat that would be encountered while sampling.

The electrical apparatus (Fig. 1) consisted of a rectifier bridge, a capacitor, a 9-V battery, an opticoupler, and a power MOSFET transistor. A rheostat was used to regulate the AC power source. The bridge rectifies the current into and deposits a charge on the capacitor, thereby creating a DC source. A signal generator was used to control the opticoupler, which in turn controlled the gate of the MOSFET and primary DC source by means of the 9-V circuit. All electrodes were made of stainless steel. The only variable was the electrode configuration, each configuration consisting of a particular combination of electrode shapes and locations. These included small 6.5 cm^2 plates, 1.5-mm diameter braided wire in which a 2.5-cm length of the plastic insulation had been removed every 3 cm, or a combination of the two. The electrode configurations and the general experimental set up are shown in Figure 2.

To determine if the number of captures between electrode configurations were significantly different, each trial of three animals was treated as a replicate in a one-way analysis of variance, with the number of animals captured in each trial as the variable. Similarly, the capture time of the first, second, and third animal in each trial was treated as a replicate and a one-way analysis of variance was performed separately for each emergence. Differences between means were tested with the LSD post-hoc test.

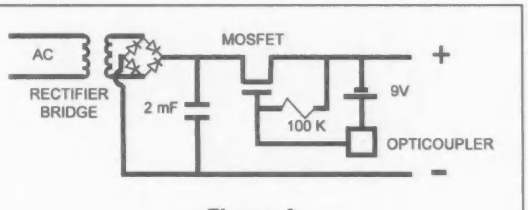

Figure 1

Circuit drawing of the electrofishing device (DC source in Fig. 2) used in experiments to determine electrotaxis and capture effciency in early benthic-phase American lobsters, *Homarus americanus*.

Results and discussion

Preliminary behavioral observations in open tanks without shelters or substrate showed that a wide size range of lobsters (5–50 mm carapace length) reacted to the electric current in a similar manner. This included an initial period of agitation of up to several seconds in which the animal appeared to become aware of the stimulus. This was followed by reorientation of the animal to face the cathode, commencement of involuntary tail flicking, and a resultant movement towards the anode. Animals of different sizes tended to react somewhat differently to the same input voltage. Larger animals (>30 mm carapace length) tended to struggle and often managed to escape the electric current. Once escaped, these animals could usually be re-entrained and induced to reach the anode by increasing the current strength and thus the tail flicking reaction. Overstimulation resulted in the animal lying motionless for several minutes after the current had been switched off. All animals that were affected in this way revived after a few minutes, apparently without ill affects. Small EBP (<10 mm) animals nearly always became motionless, usually lying on their backs, upon reaching the anode when it was situated on the substrate. If the electrode was elevated above the substrate, EBP animals gathered below it and remained motionless, but upright. When the current was switched off, they quickly escaped. EBP animals always reached the anode more quickly than large animals. In many cases the reaction was immediate and the anode was reached in less than a second. Mortalities of experimental animals (pre- and postexperimental) that could not be attributed to accidental mishandling were negligible (total of 3) during the period of observation (60 d).

We concluded that American lobsters exhibit a true electrotaxis, i.e. where an animal in a DC field is compelled to swim to the anode through involuntary muscular contractions. Electrotaxis is well known in fish (Lamarque, 1990), but has rarely been described in crustaceans. Saila and Williams (1972) observed tail muscle contractions in American lobsters subjected to currents (<38 V input), but no taxis was evident. Stewart (1974) concluded that similar tail

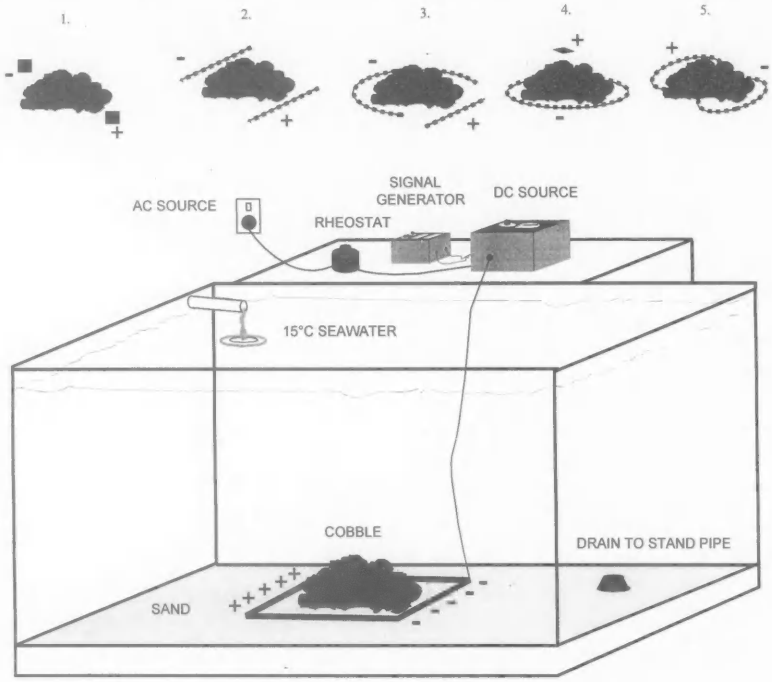

Figure 2

Laboratory setup (bottom) used to determine electrotaxis in early benthic-phase American lobsters *Homarus americanus* and capture efficiency of five electrode configurations (top).

flicking in *N. norvegicus* was not involuntary, but rather the animal's natural escape reaction induced by the electric stimulation. We have found only two reports of electrotaxis in crustaceans in which tail flicking and movement toward the anode were observed: one for the penaeid shrimp Penaeus duorarum (Higman, 1956) and the other for the rock lobster, *Panulirus cygnus* (Phillips and Scolaro, 1980).

It was apparent from these observations that the strong electrotactic response of EBP lobsters could be used to develop a quadrant-like field-sampling device. Table 1 gives the results of experiments with five different electrode configurations and EBP animals sheltered under cobble on sand substrate. These tests confirmed the unidirectional nature of the electrotaxis. Of the 81 (59%, n=137) animals that emerged from the cobble shelters, all moved directly to the anode. There was a significant difference between electrode configurations in the mean number of animals caught (ANOVA, P<0.001). The best capture rate (2.6 animals per trial, or 85% of the total population) was obtained with a semicircular cathode, straight anode and horizontal configuration (configuration 3 in Fig. 2), and the worst capture rate (0.8 animals, 25% of the population) was obtained with the circular cathode, plate anode, and vertical configuration (configuration 4 in Fig. 2). There was a significant difference between electrode configurations in mean capture time for the first animal (ANOVA, P=0.008, LSD post-hoc test) but no significant differences in capture times for the other two animals in each trial. Animals tended not to emerge at the same time but in sequence, with the first, second, and third animals emerging after an overall average of 26.3, 51.6, and 64.5 seconds. In all trials combined, one animal was caught in 91%, two in 60%, and all three in 23% of the trials. The lower and slower capture rate of the second and third animals in each test is probably related to the position of the animals in the rock pile. The EBP lobsters placed in close proximity exhibit intense aggressive behavior (Lawton and Lavalli 1995), which would tend to result in an overdispersed distribution within a bounded habitat like the test rock pile. In this situation some animals will be closer to the anode, and

Table 1

Results of electrofishing experiments with the five electrode configurations and cobble shelters on sand shown in Figure 2. The pulse frequency, duty cycle, and input voltage was 100 Hz, 50%, and 50 V, respectively, in all cases.

Electrode configuration	No. of animals[1]	No. of trials[1] (n)	Percent moving to		Mean no. captured	Percent captured	% of trials capturing			Mean capture time (sec) by order of appearance		
			anode	cathode			1 animal	2 animals	3 animals	1st animal	2nd animal	3rd animal
1	39	13	100	0	1.23 ± 0.60	41	92	31	0	66.8 ± 75.2	72.5 ± 73.7	n/a
2	39	13	100	0	2.08 ± 0.76	74	100	85	31	4.4 ± 6.1	57.5 ± 50.4	24.0 ± 19.8
3	27	9	100	0	2.56 ± 0.73	85	100	89	67	13.3 ± 12.0	42.6 ± 40.5	102.0 ± 60.4
4	24	8	100	0	0.75 ± 0.89	25	50	25	0	37.0 ± 34.5	80.0 ± 99.0	n/a
5	9	3	100	0	2.33 ± 0.58	78	100	100	33	1.0 ± 0	7.3 ± 11.0	1
Overall average						59	91	60	23	26.3	51.6	64.5

[1] Note that three animals were used in each trial.

these would tend to be caught more quickly than those farther away. Animals farther from the anode have a lower probability of a clear passage through crevices and a greater probability of being caught in a "dead end" before emerging from the rock pile.

It is apparent that electrofishing is a potentially useful method for sampling EBP lobsters. However, some additional research is necessary before a practical field sampler can be developed and tested successfully. Our study, although using the most common EBP lobster habitat, did not examine other habitats (e.g. eelgrass, mud) or variations of the common habitat, such as different rock sizes and associated crevices, or different thicknesses of cobble. Although the tedium associated with the existing sampling methods could be reduced significantly by using a diver-operated electrosampler, the most cost-effective and efficient sampler would be operated from a small boat without the need for divers. Conceivably, a sampling device that combines the electrotactic response of EBP lobsters with a bottom-to-surface water pump (e.g. Bergstedt and Genovese, 1994) could fulfill these requirements. Finally, it should be noted that the device described was designed only for use in test tanks insulated from the operator. The use of electrofishing devices in saltwater by divers, although quite safe (Stewart and Cameron, 1974), does require special precautions from an engineering as well as a personal safety perspective.

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Changes in the probability density function of larval fish body length following preservation

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The influence of body size on physiological and developmental processes during the early life history of fishes has been clearly demonstrated (Miller et al., 1988; Houde, 1989; Pepin, 1991). Because of this and to provide a direct comparison of field collections with laboratory observations that often use measurements of fresh specimens, numerous studies have quantified the effects of preservation and handling on the length of larval fish (Table 1). Most of the research has used laboratory-reared animals for which changes in length are assessed using either comparisons among treatments (i.e. ANOVA) or departures from a one-to-one relationship (i.e. regression) (Table 1). Shrinkage in length is the predominant response to preservation (Table 1), and the amount of shrinkage is influenced by handling (Theilacker, 1980, 1986; Theilacker and Porter, 1995; Fox, 1996).

Changes in larval body length due to preservation are relatively small (3–15%) although variations of up to 1 mm are not uncommon (Table 1). The contrast among species led Jennings (1991) to suggest that specific correction factors would be required. An alternative was Hjörleifsson and Klein-Macphee's (1992) simple model of the relative change in larval lengths, based on a review of previous studies, which showed clear evidence of the effects of body length and preservation time on shrinkage. Of course, as with any such review, the effects of unaccounted for or confounding variables are unknown (Pepin and Miller, 1993). However, Hjörleifsson and Klein-Macphee (1992) predicted a maximum mean shrinkage of ~15% for the smallest larvae (~2 mm) followed by an exponential decrease in relative shrinkage with increasing length. This raises an important point. Although differences in mean larval body length may appear significant from a statistical perspective, the importance of correcting for the effects of preservation are most pronounced at the level of the individual because morphological measurements are used in the analysis of each larva's physiological condition (e.g. Theilacker and Porter, 1995) to assess the relative state of a population. Even small changes in length resulting from shrinkage can create important biases at this level of analysis. In contrast, the small relative effects of preservation on body length (Hjörleifsson and Klein-Macphee, 1992) is unlikely to substantially influence estimates of length-frequency distributions.

Fundamental issues yet to be addressed in the assessment of larval shrinkage include 1) the effect of preservation on the distribution of larval length measurements within a given length interval rather than the mean, and 2) the contribution of investigator-induced error on that distribution. The former point is of particular importance because the application of correction factors to individual larvae must maintain the status of that animal in relation to others within the population. Investigator-induced error may be equally important. Few studies have attempted to quantify the variance in repeated estimates for a given operator (Jennings, 1991; Hjörleifsson and Klein-Macphee, 1992; Fox, 1996) and none have contrasted bias and variance among operators. Our failure to address these questions to date probably results from 1) the small sample sizes (i.e. generally <100) presented in most studies of the effects of preservation (Table 1), and 2) the fact that usually only a single investigator is involved in making the measurements of the larvae. Nonetheless, these issues are important because they provide the basis for narrowing the possible sources of error in interpretations of physiological processes that influence ichthyoplankton population dynamics.

In this study we report on an evaluation of the shrinkage effects of preservation on several species of larval fish collected as part of a field study. We consider changes in both the mean and variance of the distribution of individuals within narrow length intervals and assess the null hypothesis that there are no differences among species. We also

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Table 1

Summary of studies dealing with the effect of formaldehyde preservation on the length of larval fish. Under results the various symbols are S = shrinkage in length (mm); L = length before preservation; P = length following preservation; and CI = 95% confidence interval. Levels of precision recorded in either length range or results are those reported by the authors. With one exception, our summary of data reported from laboratory studies did not include simulated capture.

Species	Length range (mm)	Formaldehyde solution	Measurement method	Analysis	Sample size	Result	Source of larvae	Reference
Clupea harengus pallasi	8–26	3.7% with calcium borate or sodium borate	Micrometer	ANCOVA	$n = 120$	$S = 0.564 + 0.016\,L$	Laboratory	Hay, 1982
Clupea harengus pallasi	12–22 8–10	4%	Micrometer	ANOVA	$n = 326$ $n = 88$	Significant shrinkage	Sea–caught (dip net) and laboratory	Schnack and Rosenthal, 1978
Clupea harengus	9–20	4% with 2.5% sodium acetate trihydrate	Image analysis	ANOVA and regression	$n = 49$	$L = 1.765 + 0.867\,P$	Laboratory	Fox ,1996
Clupea harengus	7.75–9.17 13.1–17.4	0.75–3.7% in 15 or 34 ppt sea water	Micrometer	None	$n = 20$–50	7–14% shrinkage 3–7% shrinkage	Laboratory Sea–caught	Blaxter, 1971
Coregonus albula	8–10	4% neutralized with hexametylentetramin	Micrometer	ANOVA	$n = 9$–15	Significant shrinkage	Laboratory	Karjalainen, 1992
Dicentrarchus labrax	10–18	4% with 3 g/l sodium acetate trihydrate	Micrometer	ANOVA	$n = 109$	7% shrinkage (CI = –2 to 16%)	Laboratory (simulated capture)	Jennings, 1991
Engraulis mordax	3.9–21.6	2.2% buffered	Micrometer	Regression	$n = 61$	8% shrinkage (SD = 3%)	Laboratory	Theilacker, 1980
Gadus morhua	4–5	3.7% in 50% sea water	Micrometer	None	$n = 10$	12% shrinkage	Laboratory	Yin and Blaxter, 1986
Mallotus villosus	4.6–19.6	2.2% buffered	Micrometer	Regression	$n = 113$	$L = 0.36 + 1.016\,P$	Field (bongo)	Kruse and Dalley, 1990
Merluccius bilinearis	3.7–14.4	1.5% neutralized	Micrometer	Repeated measures ANOVA	$n = 83$	4.3% shrinkage	Sea–caught (bongo)	Fowler and Smith, 1983
Merluccius productus	4–5	1.1%	Micrometer	None	$n = 3$	8.9–40% shrinkage mean =15–20%	Laboratory	Bailey, 1982
Pagrus major	5–7 13–19	3.7% at pH 4.3	Micrometer	None	$n = 7$ $n = 16$	7–12 % shrinkage 3–7% shrinkage	Laboratory	Takizawa et al., 1994
Paralichthys olivaceus	7–11 12–19	3.7% at pH 4.3	Micrometer	None	$n = 18$ $n = 4$	9–16% shrinkage 2–12% shrinkage	Laboratory	Takizawa et al., 1994
Paralichthys lethostigma	9.49–13.05	1.48% buffered	Micrometer	Repeated measures ANOVA	$n = 72$	5–10% shrinkage in sea water	Sea–caught (Live trap)	Tucker and Chester, 1984
Platichthys flesus	3–4	3.7 % in 50% sea water	Micrometer	None	$n = 11$	11% shrinkage	Laboratory	Yin and Blaxter, 1986
Pleuronectes americanus	3–8.5	0.75%	Image analysis	Pairwise and regression	$n = 102$	$P = -0.20 + 0.92\,L$	Laboratory	Hjörleifsson and Klein–MacPhee, 1992
Sardinops caerulea	3.45–6.19	1.1% buffered	Micrometer	Regression	$n = 75$	$P = -0.26 + 0.9724\,L$	Sea–caught	Farris, 1963
Stizostedion vitreum	9–21	1.9% with sodium borate	Micrometer	Regression	$n = 80$	$L = 0.087 + 1.014P$	Laboratory	Johnston and Mathias, 1993
Theragra chalcogramma	4.2–20.0	1.85%	Micrometer	ANCOVA	$n = 42$	$L = 0.344 + 1.021\,P$	Laboratory	Theilacker and Porter, 1995
Trachurus symmetricus	3.35–4.10	1.85% buffered	Micrometer	None	$n = 13$	4% shrinkage	Laboratory	Theilacker, 1986

evaluate the magnitude of intra- and interoperator differences in performance for repeated measurements of the same specimens.

Materials and methods

The study was conducted on Conception Bay, Canada (47°45'N, 53°00'W), during the period of 12 July to 4 August 1995. Sampling was performed daily from CSS *Shamook* (23-m boat length) at a single site near the head of the bay.

Larvae from a number of species were obtained from vertical plankton hauls made with a square trawl 4 m long with a 4-m^2 mouth fitted with 333-µm mesh nitex and an oversize codend 20 cm in diameter and 30 cm long. The net was lowered to a depth of 20–30 m and retrieved at a rate of 1 m/s. Net design and deployment protocol were chosen to minimize trauma to larvae. On deck, the net was washed and the codend contents poured into a 20-L plastic bucket. Live and freshly dead ichthyoplankton were immediately sorted with flexible forceps and transferred to petri dishes filled with chilled seawater. Moribund larvae, indicative of death or extremely poor condition prior to capture (O'Connell, 1981; Otto and Boggs, 1983; Takizawa et al., 1994), were excluded from our samples to avoid possible bias. Each larva was assigned an indentification number, tentatively identified to the lowest taxonomic level possible, and recorded on videotape with a camera mounted on a Wild M3C dissecting microscope (S-type mount, 0.5× objective). Individual larvae were immediately transferred into 1.5 mL microcentrifuge tubes filled with 2% buffered formaldehyde. Identifications were confirmed in the laboratory and standard lengths were determined to the nearest 0.1 mm using an Optimas© image analysis system. Measurements of the video-recorded fresh standard lengths were performed at the Northwest Atlantic Fisheries Centre by an operator with more than 10 years of experience in the study of larval fish. All laboratory analyses performed on preserved larvae were conducted approximately five months after the sampling cruise at Queen's University by a novice operator with less than 1 year of experience in the study of larval fish. Each preserved larva was extracted from its microcentrifuge tube, videotaped in a manner identical to that employed for recently captured larvae, and measured (standard length) with an Optimas© image analysis system. All measurements were performed by clicking on a series of points through the centre of the head and along the notochord.

To contrast the precision and accuracy of length measurements, the experienced operator repeated a set of measurements on a sample of randomly selected larvae from the initial videotape records. In addition, a random subsample of 72 preserved capelin larvae (*Mallotus villosus*) were selected from the collection for replicate measurements by the experienced and novice operators. In each instance, both operators independently videotaped each larva for both the initial and repeated measurements. In addition, the experienced operator performed duplicate measurements on approximately one half of the samples measured by both operators. All measurements were performed with only knowledge of specimen number and magnification level.

We evaluated individual differences in body length following preservation ($\Delta l = l_{preserved} - l_{fresh}$). For analysis, data were binned into 1-mm length intervals for fresh specimens (e.g. $1 \leq \times < 2$). The hypothesis that there was no significant difference in mean body length ($H_0: \Delta\bar{l} = 0$) was evaluated by using a two-sided t-test. Comparison among species was accomplished by using an ANOVA ($H_0: \Delta\bar{l}_1 = \ldots = \bar{l}_n$, for species 1 to n). A species was included in the analysis only if there were at least three specimens within a length interval. Homogeneity of the variances in fresh (f) and preserved (p) larval lengths within each length interval was assessed by using a one-sided F-test of the null ($H_0: s_f^2 >= s_p^2$) and alternative ($H_A: s_f^2 < s_p^2$) hypotheses. Changes in individual rank, within a length interval, were assessed by using Kendall's rank correlation coefficient (τ). Operator precision and accuracy were evaluated by using general linear models.

Results

Operator accuracy

The experienced operator exhibited consistent performance in repeated measurements of both fresh and preserved capelin larvae (Fig. 1; Table 2). Regression analysis of the independent measurements by the experienced operator showed no significant departure from an intercept of 0 and a slope of 1 for both fresh and preserved specimens (Table 2). Residual variances for the two treatments were not significantly different ($F_{40, 38}$=1.1, P>0.05).

Comparison of measurements by experienced and novice operators revealed no significant bias on the part of either operator although the results did approach significance (0.1>P>0.05) and the slope was not significantly different from 1 (Table 2). However, the residual variance about the novice-experienced operator regression was significantly greater than the residual variance of repeated measurements

made by the experienced operator ($F_{72, 38}$=4.61, P<0.001).

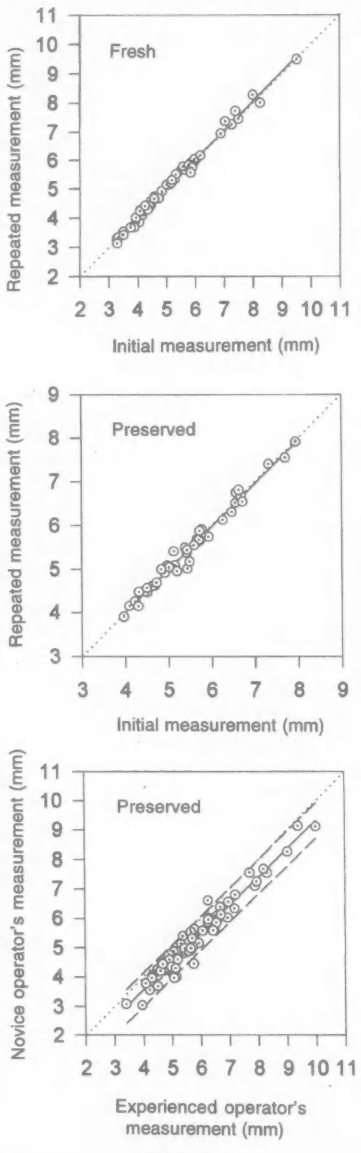

Figure 1

Comparison of repeated measurements of the experienced operator on fresh (top panel) and preserved (center panel) specimens as well as the comparison between experienced and novice operators (bottom panel). Solid lines represent least squares regressions (Table 2). Dotted lines show the 1:1 relationship. Dashed lines in the lower panel show the 95% prediction intervals.

Changes in body length

A total of 1179 larvae representing 9 different species were used in our analyses. Within each length interval, the total number of specimens available ranged from 10 to 281 individuals, representing 1 to 5 species (Table 3).

Within 1-mm length intervals, preservation resulted in significant increases in body length for individuals 3–6 mm fresh standard length and significant decreases in body length for individuals >7 mm fresh standard length (Fig. 2, Table 3). In six instances there were also significant differences among species in preserved body length (Table 3). For fresh length intervals between 5 and 9 mm there was consistency in the order of species; preserved specimens of *Hippoglossoides platessoides* were larger for a given length interval than *Ulvaria subbifurcata* and *Mallotus villosus*. However, above and below the 5–9 mm length intervals there was variation in the order of species. In the larger size classes (≥12 mm), preserved *Stichaeus punctatus* and *Gadus morhua* were larger than *Clupea harengus* and *Hippoglossoides platessoides*.

The initial variance of fresh standard lengths within each length interval ranged from 0.043 to 0.088 mm^2, whereas the variance of preserved standard lengths of these same individuals was significantly greater (Table 3) and ranged from 0.18 to 3.5 mm^2 (Fig. 3). Furthermore, the variance of the preserved length measurements increased significantly with increasing fresh length (r^2=0.70, P<0.01, n=15) (Fig. 3).

Kendall's correlation coefficient (τ) revealed that individual larvae remained at the same rank about 1 time in 3 (Fig. 4). This effect increased (i.e. 1 time in 4 or 5) with increasing fresh length.

Discussion

Changes in body length of larval fish due to handling and preservation are neither uniform nor consistent among individual animals: there is substantial variation in reaction to both handling (no matter how gentle) and preservation and variation is greatest in absolute terms for larger larvae.

No previous study (Table 1) has employed sample sizes large enough to permit the evaluation of changes in the distribution or rank of individual larvae within small length intervals. We found clear evidence that changes in body length can be more substantial than previously estimated by means of analyses applied to a broad range of sizes. Despite significant changes in body length for most length intervals, our results show that 1) variation about

Table 2

Results of the comparison of initial (I) and repeated (R) measurements on fresh and preserved larvae by the experienced (E) and novice (N) operators. Numbers in square brackets represent the standard error of the intercept (α) and slope (β). The sixth and seventh columns show the test of the hypotheses that the intercept is not significantly different from 0 and that the slope is not significantly different from 1.

Treatment	Initial	Repeat	Regression ($y = \alpha + \beta x$)	F-Value	t-value $H_0 : \alpha = 0$	t-value $H_0 : \beta = 1$	Residual variance
Fresh	E	E	$R = 0.074\ [0.128] + 0.983\ [0.0229]\ I$	$F_{1,40}$=1848, $P < 0.001$	0.58, $P > 0.05$	0.74, ns	0.020
Preserved	E	E	$R = 0.113\ [0.126] + 0.977\ [0.0228]\ I$	$F_{1,38}$=1833, $P < 0.001$	0.90, $P > 0.05$	1.01, ns	0.018
Preserved	E	N	$R = -0.271\ [0.149] + 0.959\ [0.0263]\ I$	$F_{1,72}$=1414, $P < 0.001$	1.81, $0.1 > P > 0.05$	1.56, ns	0.083

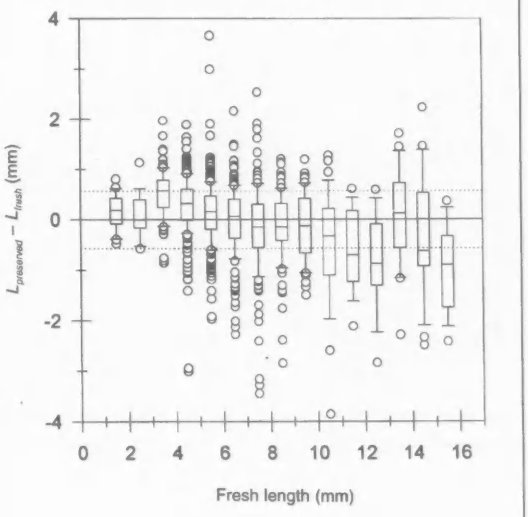

Figure 2

Box plot of the 25th, 50th, and 75th percentile of the difference in mean individual length of larval fish within each millimeter fresh length interval. Capped whiskers show the 10th and 90th percentiles and the open circles show the distribution of observations outside those confines. The dotted lines represent the 95% confidence intervals of the residual population variance from the comparison of measurement error between operators.

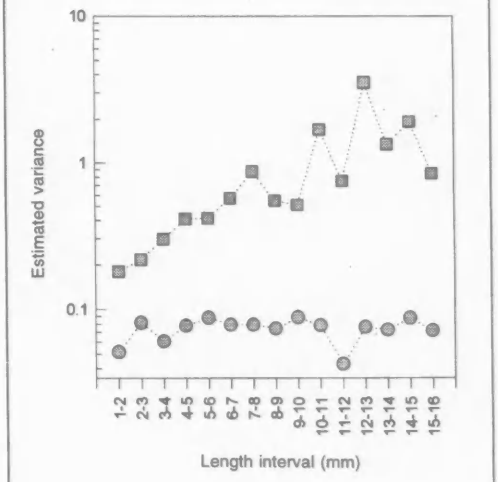

Figure 3

Variance in body length of fresh (circles) and preserved (squares) specimens within each millimeter interval.

the mean can be substantial and that 2) the relative position of an individual larva within a length interval may shift substantially.

Our findings are consistent with those of Hay (1982), Theilacker (1986), and Fox (1996) who all found that postpreservation changes in body length were greatest for large larvae. However, the marked increase in variance of preserved larval lengths in relation to the initial measurements was not caused by operator error. The residual variance of repeated measurements among operators was of the same order as the variance in fresh lengths within individual length intervals and was comparable to that obtained by Jennings (1991), Hjörleifsson and Klein-Macphee (1992), and Fox (1996). However, Fox (1996) found some evidence of increased variance with increased length, in contrast with our results. We conclude that remeasurement of larvae per se is unlikely to be a major contributor to our observation that the order of individual larvae, in relation to population estimates, is not maintained following preservation.

Our finding of postpreservation increases in body length, for individuals <6 mm SL, contrasts with most studies of the effects of formaldehyde preservation on larval fish. Fox (1996) and studies of other meth-

Table 3

Species specific mean differences in length following preservation within 1-millimeter length intervals. The number of specimens is indicated by n. Subscripts in the fourth and seventh columns refer to the species for which information was available within each length interval (i=1, . . . , n). The standard deviation of the species specific difference in length (SD) is also provided. A positive difference in length indicates expansion whereas a negative value indicates shrinkage. The last three columns present the analytical results for overall changes in length following preservation, differences among species, and homogeneity of variance between fresh and preserved specimens within each length interval.

Length Interval (mm)	Species	n	$\bar{l}_i$	SD (Δl_i)	t-value H_0:$\Delta\bar{l}=0$	F-value H_0:$\Delta\bar{l}_1=\ldots=\bar{l}_n$	F-value H_0:$s_f^2>=s_p^2$
1–2	*Pleuronectes americanus*	11	0.18	0.43	1.86, $P>0.05$	0.02, $P>0.5$	3.21, $P<0.01$
	Tautogolabrus adspersus	5	0.15	0.19			
2–3	*Pleuronectes americanus*	13	0.12	0.46	0.92, $P>0.2$	N/A	2.45, $P<0.05$
3–4	*Liparis* sp.	8	0.07	0.41	9.74, $P<0.001$	24.6, $P<0.001$	4.49, $P<0.001$
	Mallotus villosus	73	0.63	0.39			
	Pleuronectes americanus	6	–0.39	0.35			
4–5	*Hippoglossoides platessoides*	3	–0.33	0.75	6.96, $P<0.001$	2.78, $P<0.05$	4.87, $P<0.001$
	Liparis sp.	15	–0.07	0.99			
	Mallotus villosus	136	0.26	0.56			
	Pleuronectes americanus	3	0.09	0.77			
	Ulvaria subbifurcata	75	0.37	0.47			
5–6	*Hippoglossoides platessoides*	5	0.48	0.71	3.38, $P<0.001$	4.38, $P<0.01$	4.33, $P<0.001$
	Liparis sp.	7	–0.76	0.43			
	Mallotus villosus	119	0.14	0.53			
	Pleuronectes americanus	3	–0.10	0.49			
	Ulvaria subbifurcata	147	0.14	0.67			
6–7	*Hippoglossoides platessoides*	9	0.23	0.52	0.33, $P>0.5$	0.76, $P>0.2$	6.63, $P<0.001$
	Mallotus villosus	51	–0.07	0.65			
	Ulvaria subbifurcata	122	–0.01	0.70			
7–8	*Hippoglossoides platessoides*	6	0.73	0.67	2.70, $P<0.01$	4.61, $P<0.05$	10.1, $P<0.001$
	Mallotus villosus	33	–0.41	1.10			
	Ulvaria subbifurcata	96	–0.19	0.76			
8–9	*Hippoglossoides platessoides*	4	0.34	0.66	2.13, $P<0.05$	3.59, $P<0.05$	6.80, $P<0.001$
	Mallotus villosus	6	–0.79	1.54			
	Ulvaria subbifurcata	77	–0.14	0.59			
9–10	*Clupea harengus*	3	–0.12	1.08	1.71, $P>0.05$	0.13, $P>0.5$	5.35, $P<0.001$
	Hippoglossoides platessoides	7	–0.06	0.65			
	Ulvaria subbifurcata	36	–0.20	0.66			
10–11	*Hippoglossoides platessoides*	4	–1.00	2.11	2.68, $P<0.05$	0.42, $P>0.5$	19.9, $P<0.001$
	Ulvaria subbifurcata	28	–0.56	1.18			
11–12	*Hippoglossoides platessoides*	4	–0.68	0.69	2.58, $P<0.05$	0.03, $P>0.5$	16.3, $P<0.001$
	Ulvaria subbifurcata	8	–0.58	0.93			
12–13	*Clupea harengus*	3	–0.13	0.73	2.75, $P<0.05$	1.26, $P>0.5$	42.7, $P<0.001$
	Hippoglossoides platessoides	3	–1.25	0.39			
	Ulvaria subbifurcata	4	–1.09	1.29			
13–14	*Clupea harengus*	10	–0.13	0.78	0.1, $P>0.5$	2.64, $P>0.1$	16.9, $P<0.001$
	Hippoglossoides platessoides	3	–0.63	1.44			
	Stichaeus punctatus	4	0.88	0.87			
14–15	*Clupea harengus*	11	–0.81	0.97	0.8, $P>0.2$	4.74, $P<0.05$	20.2, $P<0.001$
	Gadus morhua	3	0.87	0.72			
	Stichaeus punctatus	3	0.72	1.50			
15–16	*Clupea harengus*	6	–0.80	1.00	3.78, $P<0.01$	0.82, $P>0.2$	10.8, $P<0.001$
	Hippoglossoides platessoides	4	–1.30	0.58			

ods of preservation (e.g. alcohol, freezing [Theilacker, 1980; Fowler and Smith, 1983; Kruse and Dalley, 1990; Hjörleifsson and Klein-Macphee, 1992]) have shown that individual animals may increase in

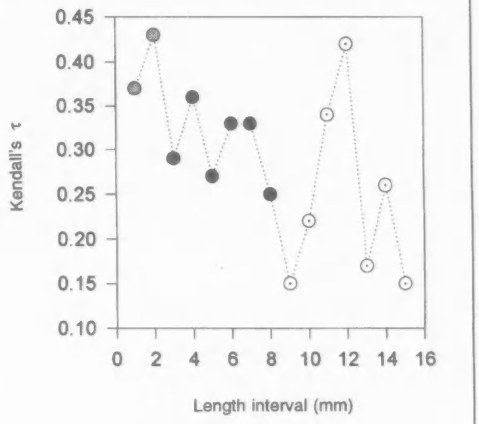

Figure 4

Rank correlation (Kendall's τ) of preserved versus fresh lengths, within millimeter intervals of fresh lengths. Open symbols represent values not significantly different from 0, grey symbols present significant values ($P<0.05$), and black symbols represent highly significant values ($P<0.01$).

length following preservation. It is important to note, however, that although our results show that the mean change in length for larvae <6 mm SL was positive, there were also numerous individuals in these same length intervals that either shrank or showed no change in body length after preservation. This finding underscores our contention that responses to preservation vary significantly at the level of the individual as well as among species.

It is possible that the capture, sorting, and preservation approaches used in this study may have led to variations in the general pattern of changes in body length. Following capture, sorting on deck may have caused a change in water temperatures. This procedure may have precipitated the death of individual larvae and resulted in contraction of body tissue in the "fresh length" measurement and consequently may have produced an apparent increase in body length following remeasurement. The source of larvae may also be an important feature to consider. Most preservation studies are based on laboratory-reared animals rather than on field-caught specimens (Table 1). Laboratory-reared animals show greater changes in length than field caught specimens (Table 1), although there is some variation about this general pattern (e.g. Theilacker, 1986).

Change in body length of marine fish larvae following capture and preservation has been attributed mainly to a breakdown of the osmoregulatory capacity of larvae, leading to a net loss of water (Ahlstrom, 1976). Simple laboratory-based studies of shrinkage have concluded that preservation results in relatively small changes in body length (see Hjörleifsson and Klein-Macphee, 1992) but that the impact of net-capture and handling is likely to have the greatest impact on changes in body length (Theilacker, 1980; Jennings, 1991; Fox, 1996). Most laboratory simulations of capture used fixed handling times; however, under field conditions it is unknown when a larva enters the net. Thus correction factors for a fixed handling time may introduce substantial error. Our sampling methods differed dramatically from those normally employed in field situations in both the duration of the residence time of larvae in the net and in the aggressiveness of capture and handling. It is therefore likely that, in comparison with other studies, the effect of capture and handling in our study was small. However, despite the possible importance of capture and handling, the interpretation of the condition of individual larvae or the distribution of population characteristics must be approached with caution.

Our results clearly show that the relative position of an individual within the size distribution of the sample is likely to change considerably following handling and preservation. Thus, attempts to correct for the effects of preservation or handling on fresh larval lengths can, in certain types of analysis (e.g. individual-based approaches to the use of morphometric measurements), introduce significant and unpredictable bias in both the data and their interpretation. There appears to be no simple solution to this problem. Conclusions as to the overall vulnerability of a fractional portion of a population to a given factor must consider the inherent variability in the distribution of measurements caused by operator, handling, and preservation-induced error.

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Sampling juvenile skipjack tuna, *Katsuwonus pelamis*, and other tunas, *Thunnus* spp., using midwater trawls in the tropical western Pacific

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Skipjack tuna, *Katsuwonus pelamis*, a highly migratory species, is one of the most important stocks for commercial fisheries in the western Pacific. The spawning ground of this species extends throughout equatorial and subtropical waters but larvae are more abundant in lower than higher latitudes (Nishikawa et al., 1978). Young and preadult skipjack tuna migrate great distances seasonally between tropical and temperate waters, yet little information is available for juvenile stages of this species.

Exploitation of skipjack tuna in the western Pacific has increased in recent years; an annual catch of 940,000 metric tons was taken in 1993 (FAO, 1995). Stock assessment and management of the species require detailed biological information on each life stage but, largely because of sampling difficulties, data on juveniles of skipjack tuna and other tunas are relatively limited compared with those on adults. Juveniles swim well and thus escape many gear: ring nets, beam trawls, or small pelagic trawls (see Methot, 1986). Other gear and light traps will not provide adequate spatial or temporal coverage (Thorrold, 1993).

Consequently development of appropriate sampling gear has been an important part of our study of the early life history of skipjack tuna and other tunas. Since 1992, we have worked to develop a new method for capturing juvenile skipjack tuna and tuna spp., namely a midwater trawl net with a large mouth opening, capable of high-speed towing. This appeared to be an excellent gear for sampling juveniles. In a trial survey, we captured large numbers of juvenile skipjack tuna and other tuna by using the midwater trawl net in offshore waters of the tropical western Pacific. This study is based on 1992–94 research cruises and confirms the effectiveness of the new midwater trawling gear. We describe the specifications of this net and its effectiveness for collecting juvenile skipjack tuna and other tuna.

Materials and methods

The midwater trawl net Tansyu has a large mouth opening and was designed to be towed at high speed. It was developed in cooperation with Tohoku National Fisheries Research Institute and Nichimo Co. Ltd., Shimonoseki, Yamaguchi. Targets for the Tansyu included skipjack tuna and other tuna, ranging in size from 10 to 200 mm standard body length (SL). The goal was to capture sufficient numbers to characterize distribution and relative abundance. The Tansyu design was based on the midwater trawl net Yoko-2, which has been used for sampling sardine by Seikai National Fisheries Research Institute, Nagasaki (Takeshita et al., 1988). The total length of the net was 71.6 m and that of the headrope and footrope was 38.6 m (see Fig. 1). The net was composed of 8 wing panels, 12 body panels, and 6 codend panels; all were made of 380 D fine polyethylene ropes. Twine diameter was between 1.91 mm (P-30) and 5.06 mm (P-210). The stretched mesh size was 1000 mm at the wings and the first panels of the body, diminishing successively to 57 mm in the seventh panels of the body. The dimension of the fishing circle was 144 × 1000 mm (where 144 = no. of meshes at mouth of net and 1000 m = mesh size at first panel of net). A codend of 60-mm mesh size was attached to the end of the body. An inner net of 30-mm and 8-mm mesh size was put inside of the codend to collect samples. Attached to the headrope were 74 floats of 300-mm diameter. A steel chain of 28-mm diameter was attached to the footrope. Buoyancy of the floats and weight of the chain were 762.4 kg and 660.4 kg, respectively. The bridles to the bottom, center, and upper wings were 18 mm in diameter and 100 m long. The expected mouth opening was approximately 20 m wide, 18 m high, at a towing speed of 4.5 knots. The net was designed for a maximum towing speed of 5 knots. The Tansyu was designed to be used with 1.7 m × 2.8 m otter doors.

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Fishery Bulletin 96:641–646 (1998).

A scale model of the Tansyu was constructed and tested in a tank at Nichimo Co. Ltd. to test its design and performance.

Research cruises were carried out from late October to early December, 1992–94. The survey covered an area from offshore of Palau past the Calorine Islands in the tropical western Pacific (Fig. 2). A 400-ton class stern trawler was chartered by the Fisheries Agency, Ministry of Agriculture, Forestry, and Fisheries, Tokyo, to conduct the midwater trawl trials.

Midwater trawling was typically conducted four times daily; standard duration of towing was approximately one hour. Towing time was defined as the duration from beginning of the net tow to commencement of warp hauling. Ten strata were occupied from near surface to 200 m, in 20-m increments of water depth; separate tows in each stratum were carried out. Depth of the net was established by noting the warp length, and towing speed was usually set 4 to 5 knots against the currents. A net-depth recorder (Furuno FNR-200) was used to monitor continuously the mouth opening and depth of the net throughout the trawling operation.

As soon as the net was brought on deck, the collection from the codend was weighed as whole wet weight; skipjack tuna and other tunas were sorted from the collection. Samples were fixed in 10% buffered formalin and preserved in 80% ethanol. All skipjack tuna specimens were identified after the cruise following the methods of Matsumoto et al. (1984). The species of tunas were identified as *Thunnus* spp. and samples of skipjack tuna and other tunas were measured individually to the nearest 0.1 mm SL with calipers.

In this report, the early life stages of skipjack tuna were defined as follows: larva: from hatching to less than 10 mm SL; juvenile: from 10 mm SL to less than 100 mm SL; and young: from 100 mm SL to less than 300 mm SL.

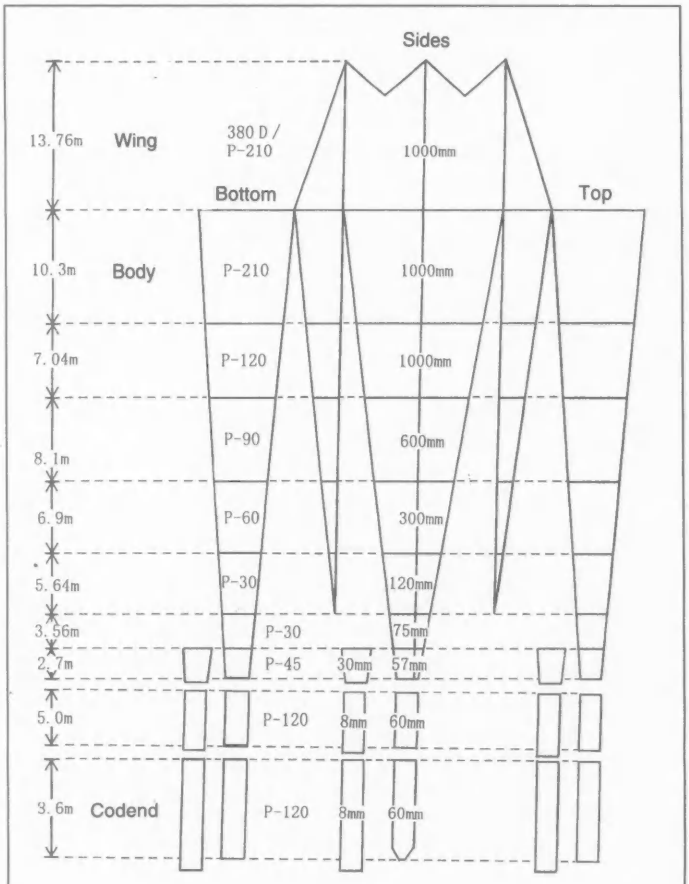

Figure 1

A schematic diagram of the midwater trawl net Tansyu that was developed to collect juvenile skipjack tuna and other tunas. The numerals on the left side indicate the length of each panel. The numerals within the diagram indicate twine size and mesh size of the net.

Results

The new trawl was deployed a total of 327 tows throughout the three years of the study. The target taxa, skipjack tuna and other tunas, were captured in 163 tows; skipjack tuna and other tunas co-occurred in 66 tows. Over four thousand skipjack tuna and other tunas were collected (Table 1). The incidence of juveniles collected remained high in all years. The maximum number of specimens collected in a single tow was over 100 juveniles of both taxa.

The diel distribution of sampling effort was 41.8% during daytime, 58.2% at nighttime (Table 2). For skipjack tuna, the mean daytime occurrence was about 5% higher than that at nighttime, and the mean daylight catch per tow was about four individuals greater than that at nighttime; a similar pattern was observed for other tuna, but the differences were not statistically significant. The whole wet weight for nighttime usually tended to be larger

than that for daytime (Table 2). Other dominant species collected at nighttime were myctophids, cephalopods, and euphausids; those taken in daylight were engraulids and acanthurids.

Size classes of skipjack tuna and other tunas were widely represented; life stages from postlarva to early young were apparent. Where SL could be measured, specimens represented 92.2% of skipjack tuna, 93.5% of other tunas. Skipjack tuna SL ranged from 7.1 mm to 171.6 mm (Fig. 3); other tunas ranged from 8.0 mm to 139.8 mm (Fig. 4). The mean SL was 25.7 mm for skipjack tuna, 27.4 mm for other tunas, with modes at 10–20 mm and 20–30 mm, respectively. Juveniles were abundant and were the dominant life stage of both species in our samples. The composition of larvae, juvenile, and young was 1.6%, 97.6%, and 0.8% for skipjack tuna, 0.7%, 98.6%, and 0.7% for other tunas. Specimens of both taxa collected at night tended to be larger than those collected during daylight. For skipjack tuna, the size of specimens during daytime ranged from 7.1 mm to 81.8 mm (average 23.8 mm); at nighttime lengths ranged from 8.1 mm to 171.6 mm (average 27.7 mm). Tunas captured in daytime ranged from 8.0 mm to 54.7 mm (average 22.6 mm), at night from 11.0 mm to 139.8 mm (average 31.7 mm). There was a significant difference in the average SL of both species between daytime and nighttime (Cochran-Cox t-test, $P<0.05$). Young skipjack tuna and other tunas were collected only at night and the number of specimens per tow was less than six. Juveniles were as just as abundant at day as at night.

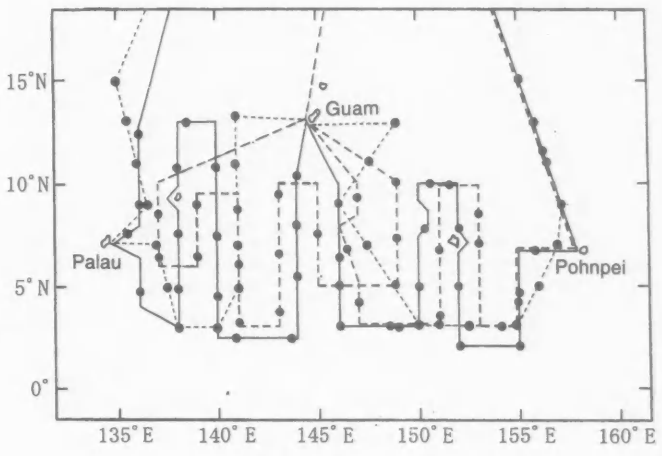

Figure 2

The sampling area. Stations (●) on the cruise tracks (---) indicate locations where the midwater trawls were deployed.

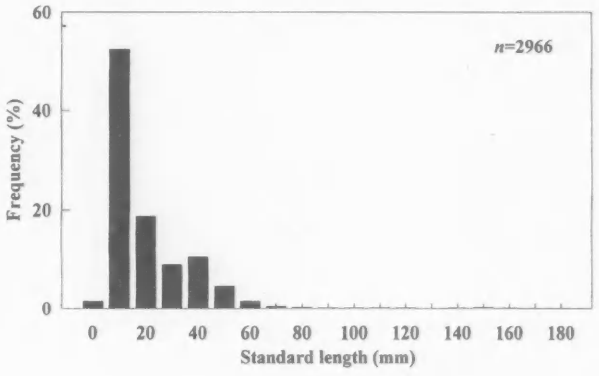

Figure 3

Length-frequency distribution of *K. pelamis* collected by the midwater trawl net in 1992–94 trial surveys.

Discussion

The midwater trawl net Tansyu made it possible to collect large numbers of juvenile skipjack tuna and other tunas during both day and night; this was not possible with the sampling gears previously available. The results of our survey demonstrate that the Tansyu was effective in collecting juveniles of skipjack tuna and other tunas.

In previous studies, various sampling gears were used for sampling larvae of skipjack tuna and other tunas (Table 3), the results of which demonstrate that

Table 1

Results of collection of juveniles and young *K. pelamis* and *Thunnus* spp. by the midwater trawl net in 1992–94. Inds. = individuals.

Species	Occurrence[1] %	Total catch (inds.)	Catch per tow[2] (inds.)
K. pelamis	49.8	3218	9.8
Thunnus spp.	27.5	1074	3.3

[1] Number of tows in which juveniles were caught/total tows × 100.
[2] Total catch of juveniles/total tows.

the maximum size of skipjack tuna and other tunas that could be collected with smaller plankton nets was about 12 mm; the usual size was 3 to 5 mm. Thus skipjack tuna and other tunas larger than 10 mm could easily escape from these gears. Davis et al. (1990) pointed out that net avoidance by larvae should be considered in calculating estimates of abundance of larval tunas.

Sampling efforts to collect juveniles (larger than 10 mm) have been reported in a few studies; King and Iversen (1962) tried to collect juvenile tunas with four kinds of trawl nets in the central Pacific, but only six juvenile tunas, size 18 to 60 mm, were collected. Higgins (1970) tried to collect juvenile tunas in Hawaiian waters using a midwater trawl net with a mouth opening 12 m × 8 m. He collected 578 skipjack tuna and 417 other tunas. Most samples rarely had juvenile stages of skipjack tuna and other tunas. Takuno and Ueyanagi (1978) tried to capture juveniles with a small pelagic trawl net in the tropical western Pacific, collecting 20 skipjack tuna and six yellowfin tuna, from 6 mm to 31 mm. These various results suggest that juvenile skipjack tuna and other tunas avoided the small trawl nets. The mouth opening and the towing speed of the Tansyu is much greater than those of small trawl nets used in previous studies. We therefore expected that the size of specimens that would be collected would be larger than those collected in previous studies if the survey area and period were chosen appropriately. Indeed, the size range of skipjack tuna and other tunas collected with the Tansyu was much greater than that collected with smaller nets. In addition, large numbers of juvenile skipjack tuna and other tunas could be collected.

Skipjack tuna and other tunas that reach the young stage are able to swim much faster than juveniles. In this study, the number of young skipjack tuna and other tunas collected was low, and these fish were caught only at night. These results indicate that net avoidance by young fish affected the number of specimens captured. The results of previous studies on swimming speeds of scombrids demonstrate that the "burst swimming speed" of adult tunas is usually from 10 to 20 fork lengths (FL) per second (Magnuson, 1978). If the burst swimming speed of young tunas (which might swim slower than adults) is, for discussion, assumed to be 10 FL per second, the speed at 20 cm FL would be estimated at approximately 3.9 knots. Therefore, the nets would need to be towed faster than 4 knots in order to sample young tunas of 20 cm FL. However, few young skipjack tuna and other tunas were collected with the Tansyu with its maximum towing speed of 5 knots. If large numbers of young skipjack tuna and other tunas were able to be collected, we would learn more about the swimming speed of young life stages of these fish and also their ecological characteristics, for example their swimming behavior and vertical distribution.

Other methods exist for collecting juvenile and young tunas, i.e. by means of light traps (Thorrold, 1993) or from stomach contents of tunas and billfish.

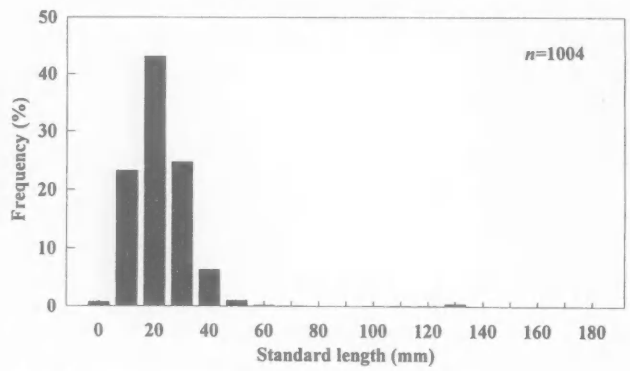

Figure 4

Length-frequency distribution of *Thunnus* spp. collected by the midwater trawl net in 1992–94 trial surveys.

Table 2

Comparison of catches between daytime and nighttime tows for *K. pelamis* and *Thunnus* spp. and total wet weight (g) of collections.

		K. pelamis		*Thunnus* spp.	
	Average catch (g)	Occurrence (%)	Catch per tow (inds.)	Occurrence (%)	Catch per tow (inds.)
Day	5405.5	52.9	12.5	28.7	3.7
Night	7010.1	48.1	8.1	27.0	3.0

Table 3

References for sampling larvae and juvenile skipjack tuna and other tunas.

Author(s)	Sampling gear	Size of sample
Strasburg, 1960	1-m ring net	3–12 mm larvae
Nishikawa et al., 1978	2-m ring net and 1.4-m ring net	<12 mm larvae
Davis et al., 1990	0.7-m bongo net and 0.7 ring net	3–11 mm larvae
Boehlert and Mundy, 1994	1-m^2 MOCNESS	2–8 mm larvae[1]
King and Iversen, 1962	1-m ring net	18–60 mm juveniles
	6-ft Isaccs-Kidd trawl	
	6-ft Isaacs-Kidd trawl	
	10-ft Isaacs-Kidd trawl	
Higgins, 1970	anchovy no. 2 Cobb pelagic trawl	7–47 mm larvae and juveniles
Takuno and Ueyanagi, 1978	midwater trawl	6–31 mm larvae and juveniles
Present study	midwater trawl	7.1–171.6 mm larvae, juveniles, and young fish
Thorrold, 1993	light trap	10–30 mm juveniles

[1] Boehlert, G. 1997. Natl. Mar. Fish. Serv., NOAA, 1352 Lighthouse Ave., Pacific Grove, CA 93950. Personal commun.

Yoshida (1971) studied the early life history of skipjack tuna using 1742 juveniles collected from the stomachs of billfishes in Hawaiian waters and the central South Pacific. Mori (1972) reported on the geographical distribution and the relative abundance of juvenile and young skipjack tuna based on collections from stomachs of tunas and billfishes in the Pacific, Indian, and Atlantic Oceans. This method was convenient and easy for sampling but produced results that should be carefully considered because they were not based on direct sampling from the habitat. Iizuka et al. (1989) using pelagic gill nets conducted research to collect young skipjack in southern Micronesian waters over a period of three years, collecting 49 young skipjack, 120 to 280 mm. The research resulted in small numbers of specimens of young skipjack tuna, and it was not clear whether the number of samples indicated the abundance of young stages.

The results of our study, in light of previous studies sampling skipjack tuna and other tunas, show that a wider size range of juveniles can be collected by using a trawl net with a larger mouth opening and by using a high towing speed, as with the Tansyu. A small ring net is appropriate for research based on sampling larvae because of its simplicity in operation. However, if it is necessary that diel patterns of vertical distribution of juvenile skipjack and other tunas be investigated, then the appropriate time and depth of towing should be selected, because ecological characteristics drastically affect the quantity of collections. Sampling of young skipjack tuna and other tunas, on the other hand, should be conducted at night with a trawl net with a large mouth opening or with a net that would minimize net avoidance by young-stage fish.

Acknowledgments

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Entanglement and mortality of bottlenose dolphins, *Tursiops runcatus*, in recreational fishing gear in Florida

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Effects of fishing gear interactions are among the most pressing issues currently being addressed by marine mammal management agencies in the United States. Information is needed on the rates and fates of entangled dolphins for evaluation of mortality caused by different fisheries. Virtually the entire emphasis of management agencies has been on marine mammal interactions with commercial fisheries; little notice has been taken of the impacts of recreational fisheries.

Along the central-west coast of Florida, near Sarasota, ongoing research initiated in 1970 on a resident community of about 100 bottlenose dolphins, *Tursiops truncatus* (Scott et al., 1990; Wells, 1991) has resulted in opportunities to examine closely the effects of interactions between dolphins and human activities, including both commercial and recreational fisheries (e.g. Wells and Scott, 1994; 1997). We report here on one case in which we removed a large quantity of fishing line trailing from a free-swimming bottlenose dolphin, and we include information on the behavior and health of the animal over the first year following entanglement and removal of the gear. We also compare the extent of commercial vs. recreational fishing interactions with dolphins.

On 4 June 1996, a seven-year-old female bottlenose dolphin ("FB03") was observed traveling alone near shore in the Gulf of Mexico off Anna Maria Island (27°33'N, 82°45'W), trailing large quantities of thin line that extended in clumps to 5 m behind the animal. The line was wrapped around the tail flukes and peduncle but did not appear to affect noticeably the dolphin's swimming ability. The dolphin (FB03) was known from birth as a member of a four-generation maternal lineage (Wells et al., 1987; Wells, 1991). She had been seen 146 times in this area prior to this incident, and was within her well-established home range. She had been observed six days earlier without any line.

This dolphin was seen next at 10:28 on 6 June 1996, in Palma Sola Bay (27°29'N, 82°40'W), several miles from her 4 June location and still within her home range. She was alone and surfacing slowly, still trailing the line. She was swimming more slowly than during the previous observation (as measured in relation to boat speed), and the clumps of line extended farther behind her, to a distance of about 8 m. Ventilations occurred at average intervals of 35.7 sec (±12.71 sec SD, n=58), comparable to previously measured rates for Sarasota dolphins (Irvine et al., 1981; Waples, 1995). The line was cutting into tissues of her flukes and peduncle. We decided to try to remove the line, assembled a team by 12:47, and approached the dolphin in our 6-m long research vessel powered by a 115-hp outboard engine. Because the trailing line followed the dolphin to the surface at each breath, we were able to reach and retrieve most of it. At 13:10 we secured the line with a boat hook, and cut all but about 2 or 3 m of line from the animal as she continued swimming. The dolphin swam rapidly and "porpoised" for about 3.7 km, left the bay, and continued to the south. We approached her again in shallow water (<2 m deep) and she maintained position, riding slowly beneath the bow of our vessel for the next 38 minutes; this is the longest recorded instance of bow-riding in the history of our research program. Her position beneath the bow afforded us an opportunity to examine closely the wounds and remaining line. Cuts around the peduncle at the insertion of the flukes and through the anterior edges of the flukes were evident. The remaining line circled the peduncle once and two freely trailing ends were draped across and extended about 1.3 m behind the

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flukes. We tried unsuccessfully a number of times to grasp the remaining line with the boat hook as the dolphin rode the bow wave. Throughout these attempts, the dolphin held her position directly below the bow, clearly watching the boat hook as it moved within several cm of her flukes, and she made no effort to move away.

The next observation of the dolphin was on 18 June 1996, on Sister Key Flats (27°27'N, 82°39'W), near where we had left her on 6 June. She was swimming normally and no line was evident, although indications of scarring were seen where the line had been. Through 1 July 1997, she was observed 33 more times and her behavior was considered normal each time. She was alone each time that she was seen while entangled; she was seen alone in only 24% of her unentangled sightings. Prior to entanglement, she was found in groups of 4.9 dolphins on average (SD=4.32, n=73). Following removal of the line, she was in groups of 4.4 dolphins on average (SD=4.56, n=30).

On 13 June 1997, this dolphin was examined by veterinarians as part of a dolphin health assessment program. The wounds from the line were well healed, but deep scars remained (Fig. 1). Her health was comparable to that at the time of her previous examination on 17 June 1994. Her weight (132 kg) was 19 kg greater than three years before. Veterinary staff considered her blood chemistry and hematology values to be within acceptable limits, and results of ultrasonic examination of organ condition were unremarkable. Thus, it appears that no long-term effects beyond scarring resulted from this relatively brief entanglement event. The depth of scars, however, suggests that her flukes could potentially have been severed if the line had not been removed. The line was determined to be 80-pound (approx.) test "squidding line," a floating-core braided Dacron line often used locally for tarpon fishing from late spring to early summer. Tarpon fishing occurs in the immediate Gulf coastal waters, especially in the area where this dolphin was first seen with the line around her flukes. A large number of snarls and cuts in the 484 m of line

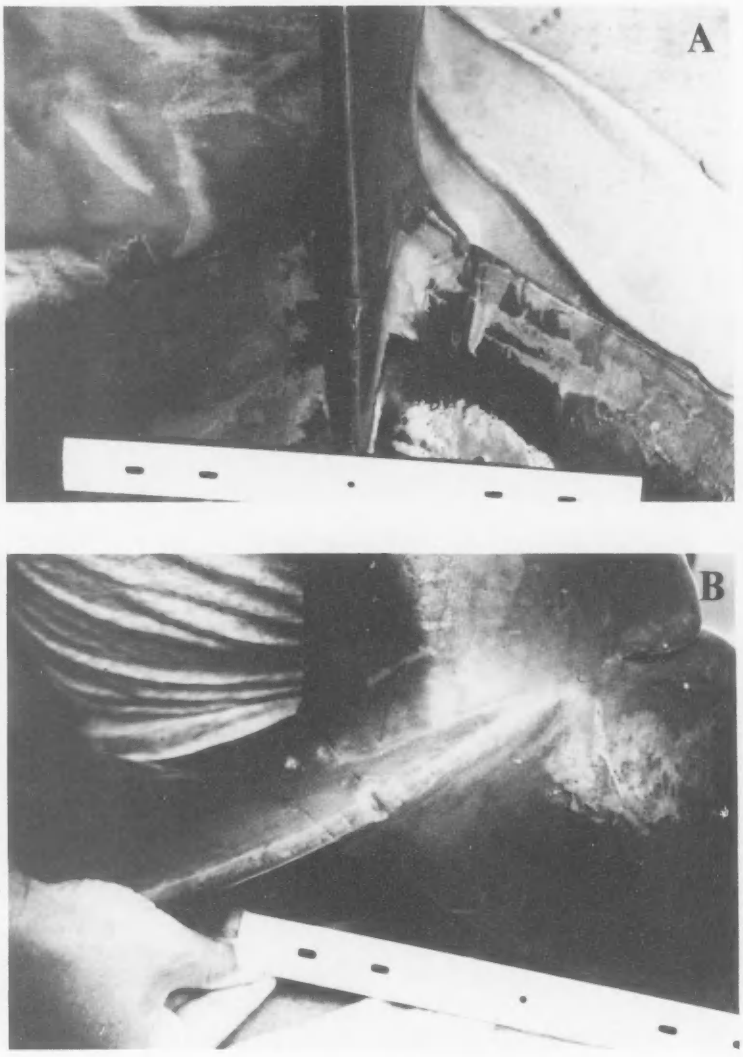

Figure 1

(**A**) Dorsal view of the scars on peduncle and flukes of the entangled dolphin (FB03) approximately one year after removal of the fishing line. (**B**) Ventral view of the scars on peduncle and flukes of the same entangled dolphin (FB03) approximately one year after removal of the fishing line.

removed suggested that it had been removed from a reel and discarded, rather than it had been actively involved in fishing at the time of entanglement.

Recreational fishing activities pose a largely ignored threat to bottlenose dolphins near Sarasota. Of 11 carcasses of resident Sarasota Bay dolphins recovered during 1993–1996, monofilament fishing line was implicated as a contributing factor in three deaths (27%). Large quantities of fishing line were found around two dependent calves (MML 9314=1.5 yr old and MML 9417=0.3 yr old). In one of these cases (MML 9314), growth of invertebrates on the line indicated that the line had been discarded prior to entanglement. The third case involved ingestion of line by an adult female (MML 9514) that had consumed a hooked sheepshead (*Archosargus probatocephalus*), as reported by Gorzelany (in press).

Wells and Scott (1994) reported that a disproportionately large number of subadult Sarasota Bay resident dolphins involved in entanglements of all kinds had been recorded through 1989 on the basis of scars observed during veterinary examinations as part of a capture-release program. More than half of the cases involved subadults; the balance were recorded from adults, but the entanglement events had occurred at an undetermined younger age. Dolphin FB03, a subadult at the time of entanglement; and the two dependent calves described above lend further support to this pattern. Similarly, Mann et al. (1995) reported on four cases of infant bottlenose dolphins becoming entangled in Shark Bay, Australia. In three of these cases, it was possible to remove the line from the semiprovisioned calves; in the fourth case, the line came free from the dolphin without human assistance. For many young animals, curiosity, inexperience, and unrefined motor skills place them at greater risk of entanglement through playful and exploratory behavior, the occurrence of which declines as the animal matures. Play may be strongly related to foraging behavior, for example, and may allow younger animals to practice, learn, and develop other behaviors that will be essential to their survival. Such behaviors may have an important role in the development of adult behaviors, but they may also be a costly practice for newborns or subadults who lack the experience of an adult.

In many parts of the world, dolphins are killed in gillnet and other fisheries (Perrin et al., 1994). It is interesting to note that in Sarasota Bay, Florida, an area of heavy recreational fishing activity, the numbers of deaths or serious injuries resulting from recreational fishing could exceed historical levels from small-scale gillnet fisheries. Gill nets were used extensively in this area prior to a state-wide ban, July 1995. Three deaths and one rescue of Sarasota resident dolphins entangled in recreational fishing gear occurred during 1993–96, but only one death (FB20 in 1976) and one rescue from gill nets (FB11 in 1985) were recorded during the 20 years prior to the 1995 gillnet ban. It should be noted, however, that stranding response coverage was uneven prior to the mid-1980s: not all deaths resulted in recovered carcasses, and not all possible entanglement events could be clearly identified as a direct cause of death, nor could they necessarily be distinguished as net or line entanglements.

Mortality and serious injury to dolphins from recreational fisheries have been largely overlooked in management, yet such mortality and injury may be important. Management actions to reduce human-related dolphin mortality are needed to address such issues, particularly in regard to the practice of discarding fishing line. Discarded line poses a risk that is somewhat analogous to that of "ghost-fishing" by commercial nets. Increased education of fishermen, through clear descriptions of the documented consequences of discarded gear is a logical, important, approach to the issue.

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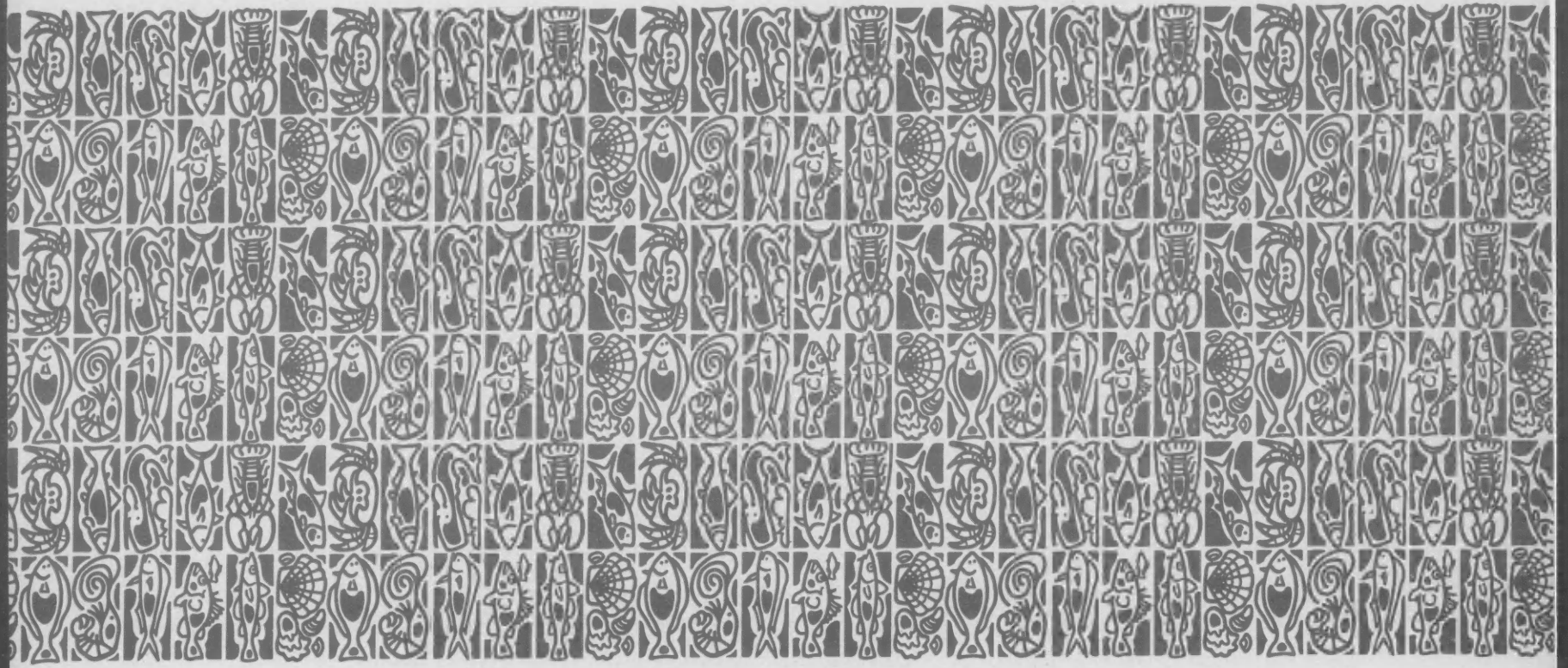
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